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OF THE SUBFAMILY
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(GAMASINA–MACROCHELIDAE)

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G. OWEN EVANS
AND
E. BROWNING

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By G. OWEN EVANS AND E. BROWNING

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SYNOPSIS

The classification of the Macrochelidae is discussed, with particular reference to the British species, and three new species are described and figured.

INTRODUCTION

The recent lists of the genera of the *Macrochelidae* follow the classification proposed by Berlese (1918), the only comprehensive work on the family. Vitzthum (1941) recognizes eight genera and eleven subgenera to which must be added the genera *Neoholaspis* Turk, 1948 (? syn : *Macrocheles* Latr. s. str.) and *Andrholaspis* Turk, 1948, and the subgenera *Cyrtocheles* Valle, 1953 and *Longicheles* Valle, 1953 of *Geholaspis* Berl. s. lat.

The British *Macrochelidae* have been investigated by Hull (1918 and 1925), Falconer (1923 and 1924) and Turk (1946). In 1918, Hull keyed ten species of *Macrocheles*, of which four were considered to be new. Later, in 1925, he described ten more new species and proposed a new name (*Macrocheles* (*Monoplites*) *oudemansii*) for *Macrocheles marginatus* Oudemans, 1901 *nec* Hermann, 1804. He used the chaetotaxy of the dorsal shield and the form of the ventral shields as his chief taxonomic criteria and although these characters have been proved subsequently to be useful key characters, his descriptions and figures are so inadequate (and often inaccurate) that a number of the species cannot be recognised with certainty.

Falconer's contribution to the study of the family consists of descriptions and figures of two new species and the erection of a new subgenus (*Dissoloncha*) of *Macrocheles*.

Turk (1946) has described one new species, *Coprholaspis anglicus*, from under wet wood at Reskadinnick, Cornwall, and has keyed British species of the genus *Coprholaspis* Berl.

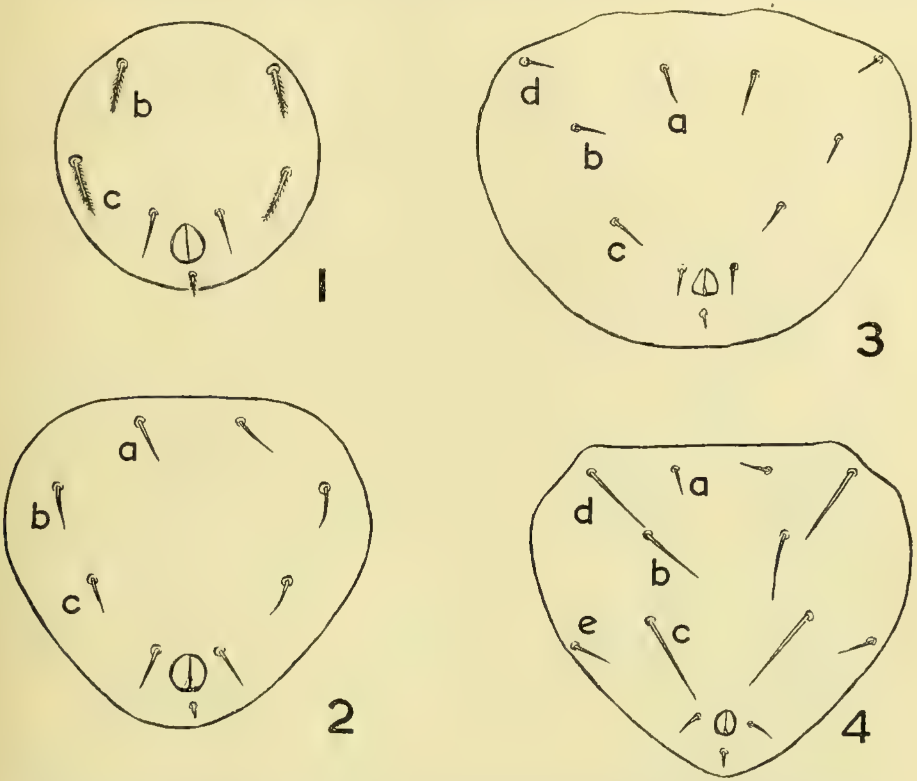
The object of the present work is to redescribe and figure the known British species of the *Macrochelinae*. We have followed Sellnick's interpretation of the species of C. L. Koch and Scopoli (Sellnick, 1931 and 1940).

EXTERNAL MORPHOLOGY

The following account of the external morphology of the British species of the *Macrochelinae* refers to the adult stages only and will serve as a general introduction to the characters of taxonomic importance used in the keys to species.

Dorsal shield : The dorsal shield in all British species is entire and covers practically the whole of the dorsum of the mite. The ornamentation of the shield shows considerable variety in form, for example, the shield may be faintly reticulated as in *Macrocheles glaber* (Müller), strongly reticulated and punctate as in *Macrocheles tardus* (C. L. Koch) or densely covered with minute tubercles as in *Geholaspis* (*Longicheles*) *mandibularis* (Berl.). Its lateral margin may be smooth or serrated.

The number of setae on the shield is remarkably constant, twenty-eight pairs in the female, except in three species (*Macrocheles montana* (Willm.), *Macrholaspis opacus* (C. L. Koch) and *Macrholaspis dentatus* sp.n.). The chaetotactic pattern and structure of the setae (whether simple, serrated or plumose) afford valuable taxonomic criteria. Sellnick (1942) and Valle (1955) have already used the chaetotaxy of the shield in their works on *Macrocheles* and *Geholaspis* s. lat., respectively. The nomenclature used for the dorsal chaetotaxy in the present work is given in Text-fig. 5. The twenty-eight pairs of setae of the female are divided into four longitudinal rows ; a dorsal series (D) of eight pairs, a median series (M) of four pairs, a lateral series (L) of six pairs and a marginal series (Mg) of ten pairs. This division is purely artificial and is not based on the post-embryonic developmental sequence. In the males, two groups can be recognized, namely, those which have the same chaetotactic pattern as the female and those which have a greater number of setae on the shield. In the latter, setae are added to the shield through its extension laterally to incorporate a number of the setae (the extra-marginal setae) normally situated on the lateral interscutal membrane.



Figs. 1–4. The chaetotaxy of the ventri-anal shield in females of *Macrholaspis* Oudemans (Fig. 1), *Macrocheles* Latr. (Fig. 2), *Holostaspella* Berl. (Fig. 3), and *Geholaspis* Berl. (Fig. 4), *a*, anterior pre-anal seta ; *b*, median pre-anal seta ; *c*, posterior pre-anal seta ; *d*, antero-lateral pre-anal seta ; *e*, postero-lateral pre-anal seta.

The anterior margin of the shield in the genera *Macrocheles, Macrholaspis* and *Geholaspis* is gently rounded with the vertical setae (D1) situated medially at a short

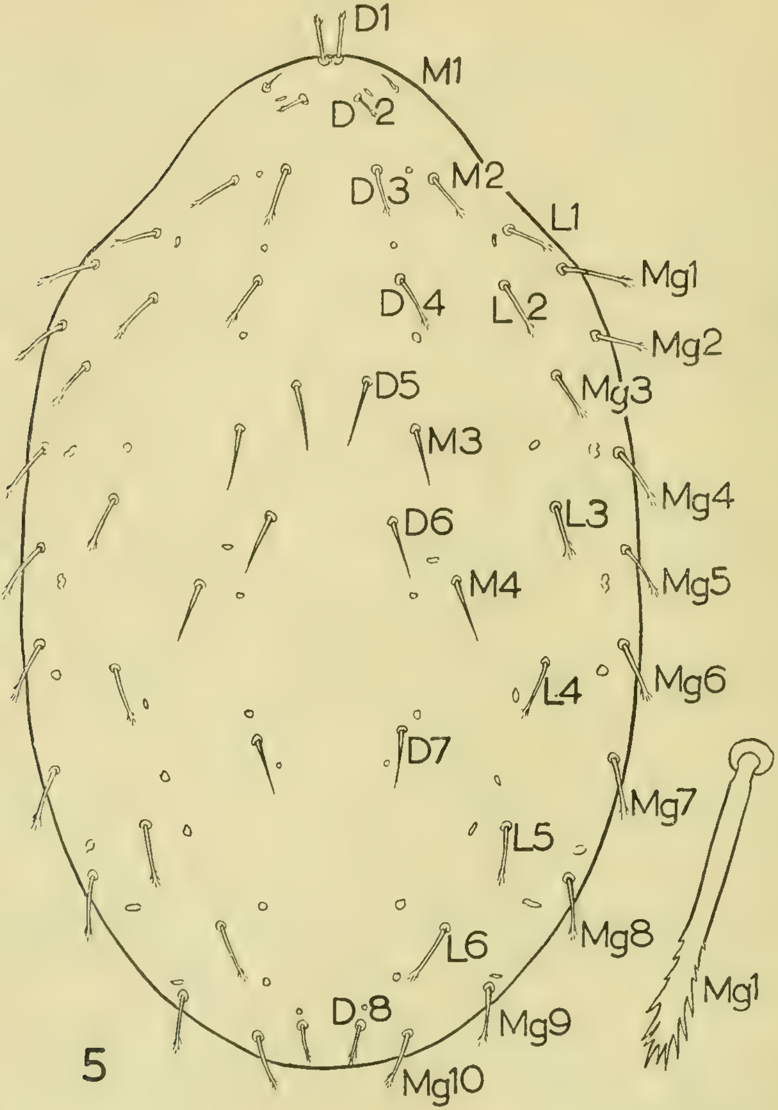

D1
M1
D2
D3
M2
L1
Mg1
D4
L2
Mg2
D5
Mg3
M3
Mg4
L3
D6
Mg5
M4
Mg6
L4
D7
Mg7
L5
Mg8
L6
Mg1
D8
Mg9
5
Mg10

FIG. 5. Chaetotaxy of the dorsal shield in *Macrocheles muscaedomesticae* (Scopoli), female. D1–D8, dorsal series; M1–M4, median series; L1–L6, lateral series; Mg1–Mg10, marginal series.

distance from the margin. In *Holostaspella*, however, the vertical setae are no longer on the summit of the shield but on an outgrowth from it (Text-fig. 82).

In addition to the setae, the shield is provided with a number of pore-like structures. There are normally twenty-two pairs of these " pores ".

Tritosternum. This structure is well-developed throughout the group and consists of a rectangular base, longer than wide, and a pair of long, pilose lacinae.

Ventral shields. In the female, the ventral shields comprise the sternal, metasternals, genital, ventri-anal and metapodals.

The sternal shield is strongly sclerotized and carries three pairs of setae (h1, h2 and h3) and two pairs of pores. The ornamentation of the shield is usually characteristic of a species or a group of species. Berlese (1918) used the ornamentation of the shield as a major character for subdividing the subgenus *Coprholaspis* and introduced a system of nomenclature for the lines and punctate areas forming the basic pattern (Text-fig. 2). The writers have referred, in the main, to a photograph of the sternal shield instead of attempting a description of the ornamentation. The metasternal shields are paired and free, i.e. they are not fused with the sternal or endopodal shields. Each bears a seta and usually a " pore ".

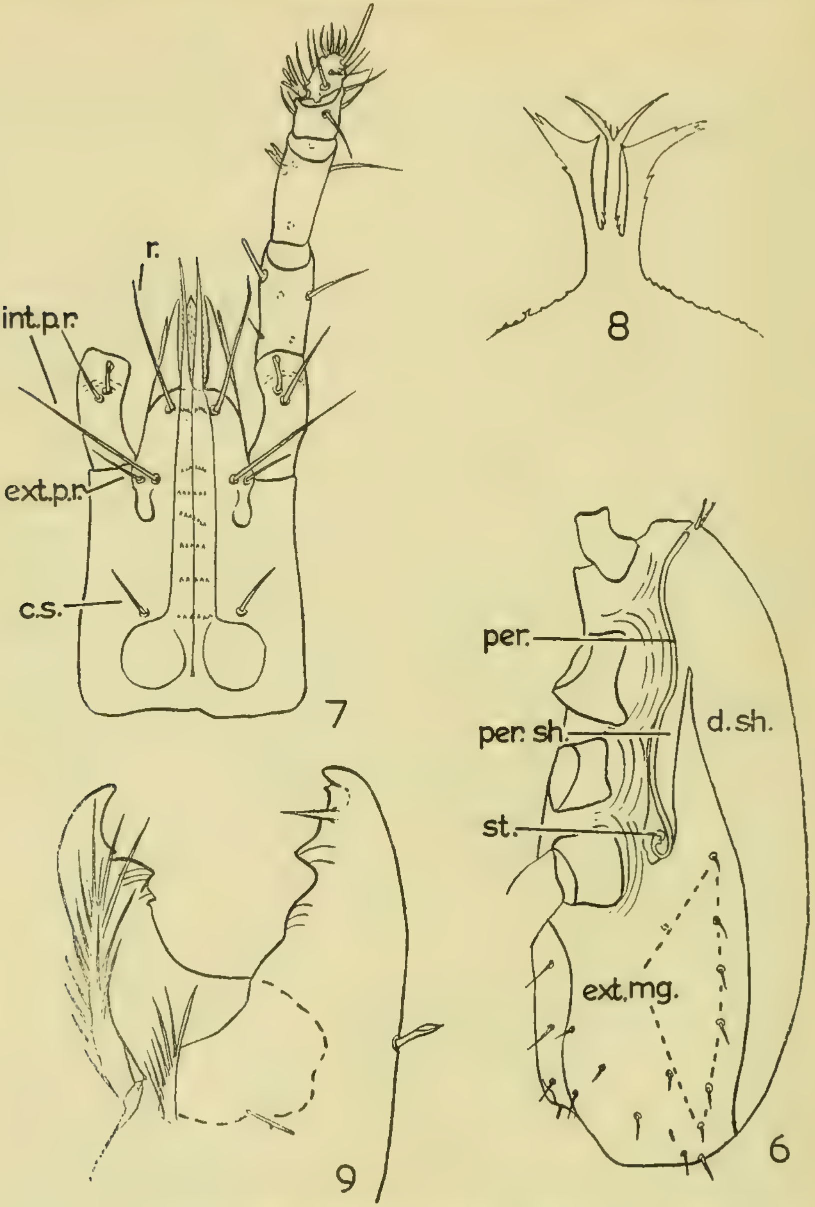
The genital shield lies between coxae IV and carries a pair of genital setae. It is invariably reticulated and punctured, and is provided with accessory sclerites as in the genus *Veigaia* Oudms. (*Gamasina–Veigaiaidae*). The lateral sclerites are usually well-developed, but the median sclerite is often only weakly sclerotized.

The region posterior to coxae IV is largely occupied by a ventri-anal shield bearing two (*Macrholaspis*), three (*Macrocheles*), four (*Holostaspella*) or five pairs (*Geholaspis*) of pre-anal setae. The nomenclature for these setae is given in Text-figs. 3–6. In addition to the pre-anals the shield bears the normal three setae associated with the anus, namely, the paired para-anals and the post-anal seta. The surface of the shield is usually reticulated and punctured. The interscutal membrane between the genital and ventri-anal shields may be provided with sclerotised platelets. The metapodal shields are relatively small and inconspicuous.

In the male, the ventral surface may be covered by a sterniti-genital shield in the region of coxae I–IV and a separate ventri-anal shield posterior to coxae IV or, by a holoventral shield, i.e. a fused sterniti-genital and ventri-anal shield. The genital orifice is prae-sternal.

Stigmata, peritremes and peritrematal shields. The stigmata, one on each side of the idiosoma, are situated between coxae III and IV. The peritremes are well-developed and extend beyond the level of coxae I. Each forms a U-shaped loop in the region of the stigma (Text-fig. 6). The peritrematal shield is fused anteriorly with the dorsal shield, but is free in its proximal half.

Gnathosoma. The gnathosoma is typical of that found in the free-living Gamasina. Ventrally, it is provided with four pairs of setae and a distinct ventral or capitular groove (Text-fig. 7). The latter has five to seven transverse rows of denticles. The corniculi are well-developed and the internal malae long and pilose. The salivary styli are also prominent. The five free segments of the pedipalp bear simple, rod-like or spatulate setae. The chaetotactic formula for the trochanter, femur and genu is



Figs. 6–9. *Macrocheles muscaedomesticae* (Scopoli), female. Fig. 6, lateral view. Fig. 7, venter of gnathosoma. Fig. 8, tectum. Fig. 9, chelicera.

Abbreviations: *c.s.*, capitular seta; *d.sh.*, dorsal shield; *ext. mg.*, extra-marginal series; *ext.p.r.*; external posterior rostrals; *int.p.r.*, internal posterior rostrals; *per.*, peritreme; *per.sh.*, peritrematal shield; *r.*, rostral seta; *st.*, stigma.

2–5–6. The specialized seta on the inner basal angle of the palptarsus is three-pronged. This segment also bears a conspicuous long, upright, rod-like seta distally.

The tectum is extremely variable in form. In the majority of the species it consists of three anteriorly directed processes. These may be free (Text-fig. 8) or each lateral process partly fused with the median (Text-fig. 31). The lateral processes may be smooth and entire or divided and serrated. The median process is usually strongly setose and bifurcate distally. In *Macrocheles superbus* Hull and *Geholaspis* s. str. the tectum is simply produced into a single anteriorly directed process, variously divided distally (Text-figs. 57 and 64).

The chelicerae in both sexes are chelate-dentate. The teeth are massive and ridged, or conical and smooth. The *pilus dentilis*, dorsal seta and pore, lyriform pore and ventral setae are well-developed. In the male the movable digit is provided with a strong spermatophoral process. This may be long and slender or short and inflated (Text-figs. 39 and 60).

Ambulatory appendages. All the legs are six-segmented with the ultimate segment incompletely divided into a metatarsus and tarsus. Leg I is without an ambulacral apparatus (pulvillus and claws) and terminates in a number of sensory setae. This is a characteristic feature of the family. Legs II–IV, however, have well-developed lobate pulvilli and claws. In the females, spurs are present on the femur and tarsus of leg II in the genus *Holostaspella* only (Text-fig. 85). The femur, genu and tibia of Leg II and often one or more segments of leg IV are spurred in the males.

CLASSIFICATION

Trägårdh (1952) divided the *Macrochelidae* into three subfamilies as follows :

" 1. Metasternal shields connected with the sternal shield through a narrow bridge *Protoholaspinae* Trägårdh, 1949
–. Metasternal shields free . . . . 2.
2. Peritrematic shields not fused with the exopodal shields *Macrochelinae* Trägårdh, 1949
–. Peritrematic shields fused with the exopodal shields . . *Areolaspinae nov. subfam.*"

The genus *Protoholaspis* Trägårdh 1949, the only member of the *Protoholaspinae*, is not a typical Macrochelid in that leg I is provided with an ambulacrum and the chelicera lacks the characteristic ventral seta. Further, Trägårdh was unable to see the structure of the specialized seta on the inner basal angle of the palptarsus, so that the exact systematic position of the genus must remain in doubt pending the re-examination of the type. The family should, therefore, be considered to consist of the two subfamilies separated in couplet 2 of the above key.

The majority of the British species belong to the *Macrochelinae* ; the *Areolaspinae* being represented by *Holaspulus tenuipes* Berl. and *Parholaspis* sp., which are introduced species that have become established in the Aroid House, Royal Botanic Gardens, Kew. The following separation of the four British genera of the *Macrochelinae* is based on Evans (1956) :

Key to genera

Females

1. Femur of leg II armed with strong spurs ; vertical setae situated on an outgrowth of the dorsal shield ; ventri-anal shield with four pairs of pre-anal setae *Holostaspella* Berl.
–. Femur of leg II unarmed ; vertical setae on the summit of the dorsal shield ; ventri-anal shield with 2, 3 or 5 pairs of pre-anal setae . . . . 2.
2. Ventri-anal shield with two pairs of pre-anal setae . . . *Macrholapis* Oudemans
–. Ventri-anal shield with more than two pairs of pre-anal setae . . . . . 3.
3. Ventri-anal shield with three pairs of pre-anal setae . . . *Macrocheles* Latreille
–. Ventri-anal shield with five pairs of pre-anal setae . . . *Geholaspis* Berl. *s. lat.*

Genus ***MACROCHELES*** Latreille

Macrocheles Latreille, P. (1829). In Cuvier, *Règne anim.*, Ed. 2, **4** : 282.
Coprholaspis Berlese, A. (1918). *Redia*, **13** : 146.
Nothrholaspis Berlese, A. (1918). *Redia*, **13** : 169.
Dissoloncha Falconer, W. (1923). *Naturalist, Lond.* : 151.
Monoplites Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9), **15** : 215.

Berlese (1918) divided the genus *Macrocheles* into four subgenera, namely, *Macrocheles* s. str., *Coprholaspis*, *Nothrholaspis* and *Geholaspis*. Sellnick (1940) has shown conclusively that *Coprholaspis* is a synonym of *Macrocheles* s. str. and, within recent years, *Geholaspis* has been given generic status. The remaining two subgenera have been separated, chiefly, by the ornamentation of the sternal shield in the female. In the majority of the species of *Macrocheles* s. str., this shield is ornamented with distinct lines or punctate lines whereas in *Nothrholaspis* the ornamentation takes the form of a network of ridges (cf. Pl. 1, fig. 3 and Pl. 3, fig. 15). This distinction is not as definite as supposed by Berlese and, as is often the case with a general character of this nature, an intermediate group, containing species which could belong to either subgenus, is apparent. In view of this, and until a more comprehensive study can be made of both sexes of the known *Macrocheles* species, especially those in the Berlese Collection, the writers feel it advisible to combine the subgenus *Nothrholaspis* with *Macrocheles*.

Ecologically, the British species of this genus may be divided into two groups : those living in dung and those inhabiting leaf litter or mosses. The former contains a number of phoretic species, e.g. *M. muscaedomesticae* and *Macrocheles glaber* (Müller), in which the shape and chaetotaxy of the dorsal shield in the male differs considerably from that in the female.

The genus *Macrocheles* may be defined as follows : Dorsal shield in both sexes entire with usually twenty-eight[1] pairs of setae and twenty-two pairs of " pores." Sternal shield in the female with three pairs of setae ; metasternal shields free. Genital shield with a pair of setae and accessory sclerites. Ventri-anal shield with three pairs of pre-anal setae in addition to the three setae normally associated with the anus. Male with sterniti-geniti-ventral shield and separate ventri-anal or with holoventral

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[1] *Macrocheles montanus* (Willmann) has twenty-nine to thirty-one pairs of setae on the dorsal shield, and in some males the number of setae may be increased through the lateral extension of the shield to incorporate a number of the extra-marginal setae.

shield. Genital orifice prae-sternal. Hypostome with well-developed corniculi and salivary styli. Pedipalps with five free segments; chaetotaxy of trochanter, femur and genu being (2–5–6). Specialized seta on the palptarsus with three prongs. Chelicerae chelate dentate with a well developed brush of setae ventro-laterally; movable digit in the male with a strong spermatophoral process. Legs I without ambulacra; legs II and often legs IV, spurred in the male.

TYPE: *Acarus marginatus* Hermann, 1804 (= *Acarus muscae domesticae* Scopoli, 1772).

Key to the Females of the British Species of Macrocheles *Latr.*

1. Setae L3 to L5 and Mg3 to Mg6 simple . . . . 2.
–. Setae L3 to L5 and Mg3 to Mg6 serrate, plumose or pencillate[1] . . . . . 8.
2. Setae D8 simple or pilose . . . . 3.
–. Setae D8 short, comb-like (Text-fig. 11); sternal shield weakly ornamented; ventri-anal shield considerably longer than broad; fixed digit of the chelicera with a row of 5 or 6 small teeth distally (Text-fig. 13) . . . . *Macrocheles pisentii* (Berl.)
3. Vertical setae (D1) stout and plumose or long and setiform (Text-fig. 22). Dorsal shield more than 600μ in length . . . . 4.
–. Vertical setae short spine-like (Text-fig. 24). Dorsal shield less than 500μ in length . . . . 7.
4. Vertical setae short and stout, plumose distally; setae D4, L1, L2, L6 and Mg1 simple (Text-fig. 17); tibia I approximately equal in length to tarsus (1 : 1·0–1·05) . . . . 5.
–. Vertical setae long setiform (Text-fig. 15) with inconspicuous serrations distally; sternal shield densely punctured; setae D4, L1, L2, L6 and Mg1 pencillate; tibia I shorter than tarsus I (1 : 1·2–1·44) . *Macrocheles rothamstedensis* sp. nov.
5. Sternal shield with deeply incised transverse median and posterior oblique lines (Pl. 1, fig. 3); dorsal setae, except D1, D4 and L2, simple *Macrocheles glaber* (Müller)
–. Sternal shield punctured, transverse median and posterior oblique lines poorly developed or absent; setae D4 simple . . . . 6.
6. Ventral shields densely punctured (Pl. 1, fig. 4); setae Mg2, Mg7, Mg9 and D8 distinctly serrated (Text-fig. 21) . . . . *Macrocheles punctoscutatus* sp. nov.
–. Sternal shield with fewer large punctures (Pl. 1, fig. 5); setae D1, D8 and L2 only serrate or pencillate . . . . *Macrocheles subbadius* (Berl.)
7. Sternal shield ornamented with large punctures (Pl. 1, fig. 6) *Macrocheles insignitus* Berl.
–. Sternal shield weakly ornamented with punctate lines (Pl. 2, fig. 7) *Macrocheles merdarius* (Berl.)
8. Dorsal shield with 29[2] or more pairs of setae (Text-fig. 27); median pre-anal seta on or slightly off the line connecting the anterior and posterior pre-anals (Pl. 2, fig. 8) . . . . *Macrocheles montanus* (Willmann)
–. Dorsal shield with 28 pairs of setae . . . . 9.
9. Vertical setae situated in close proximity to each other, so that their bases are more or less contiguous (Text-fig. 5) . . . . 10.
–. Vertical setae further apart, their bases distinctly separated, i.e. at least the diameter of the setal base apart . . . . 12.
10. Lateral and marginal setae slender, plumose only in their distal third (Text-fig. 5); sternal shield with distinct lines (Pl. 1, fig. 1); lateral processes of the tectum free (Text-fig. 8) . . . . *Macrocheles muscaedomesticae* (Scopoli)

[1] Except in *Macrocheles submotus* Falconer in which Mg4 is simple and Mg5 and 6 pilose.
[2] This species is characterised by having *nine* pairs of setae in the D series.

–. Lateral and marginal setae strongly plumose in their distal two-thirds ; lateral processes of the tectum partially fused . . . . 11.

11. With three pairs of platelets between ventri-anal and genital shields (Pl. 2, fig. 9) . *Macrocheles carinatus* (C. L.Koch)

–. Without platelets between ventri-anal and genital shields . . . . . *Macrocheles penicilliger* (Berl.)

12. Setae D2, Mg2 and Mg4 simple (Text-fig. 36) . . *Macrocheles submotus* Falconer

–. Setae D2, Mg2 and Mg4 plumose . . . . 13.

13. Setae M1 simple, approximately equal in length to D1 and extending beyond the bases of D2 by about one-half their length (Text-fig. 42) *Macrocheles tardus* (C. L. Koch)

–. Setae M1 simple or plumose and considerably shorter in length than D1 . . 14.

14. Dorsal shield less than 950μ in length . . . . 15.

Dorsal shield more than 1100μ in length . . . . 16.

15. Setae Mg10, approximately equal in length to D8, are about half the length of Mg9 (Text-fig. 44) ; external margin of the lateral processes of the tectum smooth anterior to the base of the median process (Text-fig. 45) ; punctate areas on the sternal shield inconspicuous . . . . *Macrocheles decoloratus* (C. L. Koch)

–. Setae Mg10 equal in length to Mg9 (Text-fig. 47) ; external margin of the lateral processes of the tectum serrate well beyond the base of the median process (Text-fig. 48) ; punctate areas on the sternal shield large, conspicuous *Macrocheles matrius* Hull

16. Setae M1 plumose and lying in line with setae D1 (Text-fig. 50) ; lateral margins of the dorsal shield coarsely and unevenly serrated (Text-fig. 51) ; ventri-anal shield considerably broader than long and characteristically shaped (Pl. 3, fig. 15) *Macrocheles plumiventris* Hull

–. Setae M1 simple and lying in line with D2 (Text-fig. 56) ; lateral margins of the dorsal shield minutely and evenly serrated (Text-fig. 55) ; ventri-anal shield considerably longer than broad . . . . *Macrocheles superbus* Hull

Macrocheles muscaedomesticae (Scopoli) Sellnick.

Acarus muscae domesticae Scopoli, J. A. (1772). *Annus. V. Hist. Nat.* : n. 125, 157.

Acarus marginatus Hermann, J. F. (1804). *Mém. Apt.* : 76, figs.

Macrocheles muscae domesticae, Sellnick, M. (1940). *Göteborg. Vetensk. Samh. Handl.* (5) **6B**, No. 14 : 78, figs.

Macrocheles muscaedomesticae, Pereira, C. & de Castro, M. P. (1945). *Arq. Inst. Biol. S. Paulo* **16** : 163, figs.

Female. Dorsal shield reticulated and bearing twenty-eight pairs of setae and twenty-two pairs of " pores " (Text-fig. 5). Vertical setae plumose in their distal third and lying in close proximity to each other. Setae D5–D7, M1, M3 and M4 simple. The remainder of the setae on the dorsal shield are pilose in their distal third. The distribution of the setae and pores is shown in the figure. Extra-marginal setae are simple (Text-fig. 6).

The sternal shield is characteristically ornamented with punctures and ridges (Pl. 1, fig. 1.) All the sternal setae are simple. The metasternal shields are free and each carries a simple seta. Genital shield, truncate posteriorly, bears a simple pair of setae and is ornamented with punctate lines. The ventri-anal shield (approx. 368 × 379μ) has a loose network of punctate lines. All the setae on this compound shield are simple. The peritrematal shield is free posteriorly ; being separated from the exopodal shields by a wide expanse of striated cuticle (Text-fig. 6). The peritreme extends beyond coxa I.

The gnathosoma is strongly sclerotized and carries four pairs of setae ventrally (Text-fig. 7). The ventral groove is provided with six or seven transverse rows of denticles. Anteriorly the corniculi and salivary stylets are strongly developed. The chaetotaxy of the five free segments of the pedipalp is normal for the free-living *Gamasina*. The specialized seta on the inner basal angle of the palptarsus is three-pronged. The lateral processes of the tectum are free ; the median process is bifid distally (Text-fig. 8). The chelicerae are massive ; the movable digit being tridentate and the fixed bi- or tridentate (Text-fig. 9).

Leg I has the tarsus (187μ) longer than the tibia (165μ).

Male. This sex and the immature stages are described and figured by Pereira & de Castro (1945).

Dimensions. Female : length 980–1014μ ; breadth 570–671μ. *Male* : length 750–900μ ; breadth 450–600μ.

HABITAT AND LOCALITY. This species is commonly found on *Musca domestica* Linn. and allied species. Pereira & de Castro (1945) state that all instars except the larval feed on the eggs of house flies. *M. muscaedomesticae* is cosmopolitan in distribution.

Macrocheles pisentii (Berl.)

Gamasus tardus var. *Pisentii* Berlese, A. (1882). *Bull. Soc. ent. Ital.* **14** : 112, fig.
Holostaspis Pisentii Berlese, A. (1887). *Acari, Myriopoda et Scorpiones, etc.*, Fasc. 76, N. 1.

Female. Dorsal shield, minutely punctured, and bearing twenty-eight pairs of setae. Vertical setae simple and well separated from each other (Text-fig. 10). Setae D8 short and comb-like (Text-fig. 11). The remainder of the setae on the dorsal shield long and sharply pointed distally. Extra-marginal setae simple.

Ventrally, the sternal shield (without distinct ornamentation) has three pairs of simple setae. Its posterior margin is strongly concave. Metasternal shields small ; setae simple. Genital shield with well-developed lateral sclerites, Ventri-anal shield (about 285 × 220μ) is considerably longer than broad. All the setae on this shield are simple.

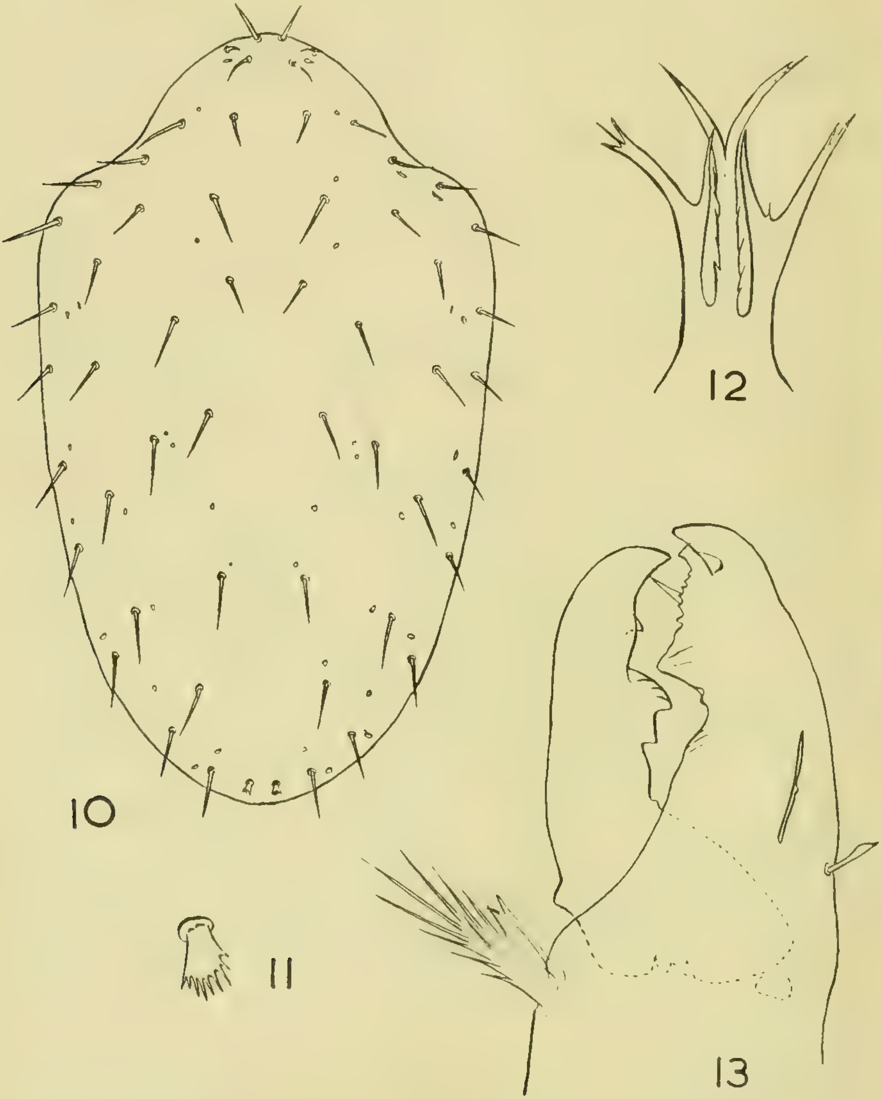
External posterior rostrals are about-one-third the length of the internals. The ventral groove has five transverse rows of denticles. The characteristic form of the tectum is shown in Text-fig. 12. The fixed digits of the chelicerae are provided with one large, grooved tooth and five or more small teeth (Text-fig. 13). The movable digit is tridentate ; the middle tooth being large and recurved.

Leg I has the tarsus (143μ) longer than the tibia (132μ). Tarsus II is provided with stout spines.

Male. Unknown.

Dimensions. Female : length 810–835μ ; breadth 490–506μ.

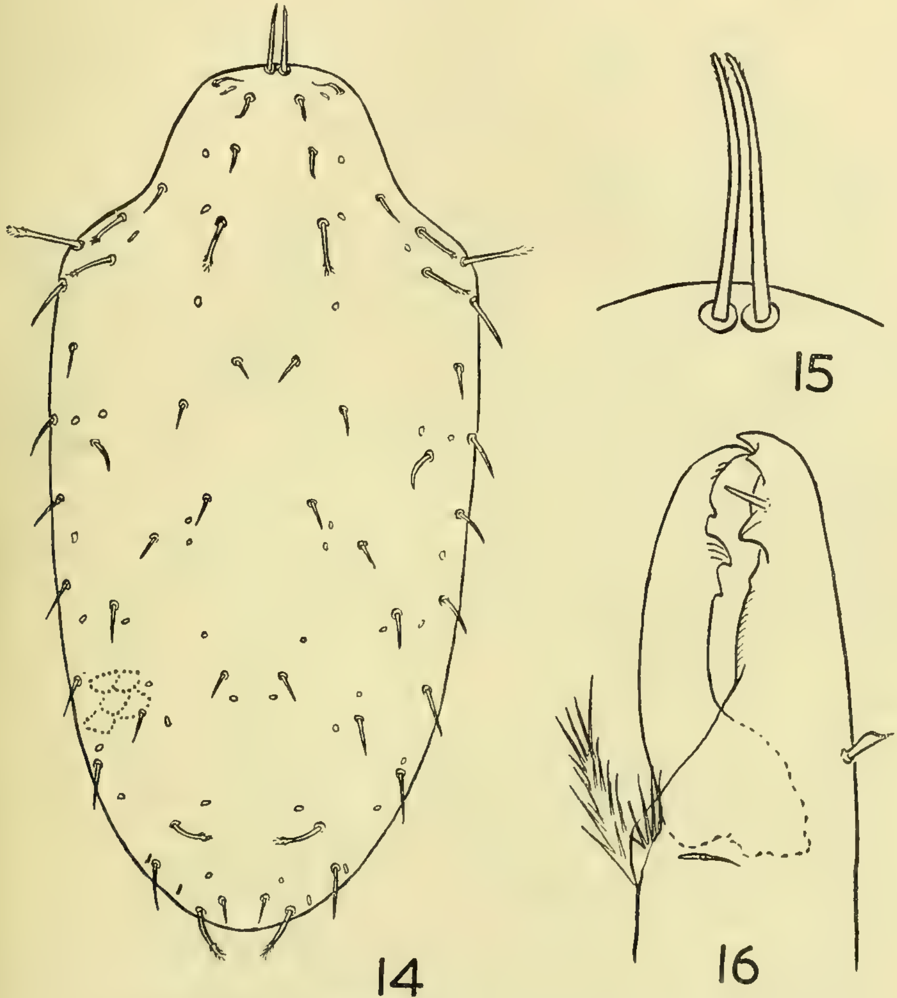
HABITAT AND LOCALITY. This species has been collected from *Scarabaeus semipunctatus* in Italy. Hull (1918) records it from a nest of *Formica rufa* at Chopwell, Durham; from moss at Ninebanks, Northumberland; and in dead leaves, Cheshire. We have not examined Hull's specimens. The above description and figures are based on specimens in the Oudemans Collection, Leiden.



FIGS. 10–13. *Macrocheles pisentii* (Berl.), female. Fig. 10, dorsal shield; Fig. 11, seta D8 enlarged. Fig. 12, tectum. Fig. 13, chelicera.

Macrocheles rothamstedensis sp. nov.

FEMALE. Dorsal shield, with twenty-eight pairs of setae and twenty-two pairs of "pores", is weakly ornamented with punctate lines forming a polygonal network (Text-fig. 14). The vertical setae are long and slightly pilose distally; their bases are almost contiguous (Text-fig. 15). Setae D4, L1, L2, L6, Mg1 and Mg10 are conspicuously pilose distally, other dorsal setae may show slight pilosity distally. All the extra-marginal setae are simple.



FIGS. 14–16. *Macrocheles rothamstedensis* sp. nov., female. Fig. 14, dorsal shield. Fig. 15, setae D1 enlarged. Fig. 16, chelicera.

The sternal shield is densely covered with punctures which tend to form a pattern of punctate lines (Pl. 1, fig. 2). All the sternal setae are simple. The smooth metasternal setae lie on small narrow shields. The genital shield, with a pair of simple setae, is truncate posteriorly and ornamented with a network of punctate lines. The lateral sclerites are strongly formed. The ventri-anal shield (approx. 250 × 198μ) is longer than broad and ornamented with a loose network of punctate lines. All the setae on this shield are simple. The metapodal shields are small and weakly sclerotised.

The venter of the gnathosoma is minutely punctured. The ventral groove is provided with five rows of denticles. Each lateral process of the tectum is free. The movable digit of the chelicera is tridentate ; the fixed digit is basically bidentate (Text-fig. 16).

Leg I (approx. 610μ in length) with the tibia (110μ) evidently shorter than the tarsus (143μ). Legs II and III with simple setae ; leg IV with plumose setae on the femur, genu, tibia and tarsus.

MALE. Dorsal shield, strongly attenuated posterior to coxae IV, bears thirty pairs of setae. The chaetotactic pattern differs from that in the female in the addition of two pairs of extra-marginal setae to the shield and the greater distance between the verticals. The ornamentation of the shield is similar to that in the female.

The venter is covered by a punctured holoventral shield bearing nineteen simple setae.

The tectum is basically the same as in the female. The fixed digit of the chelicera is tridentate and the movable is provided with two or three small teeth. The spermatophoral process is about the length of the movable digit.

Femur, genu and tibia of leg II and the femur and tibia of leg IV are spurred. Femur II and trochanter IV have small sclerotized ridges.

DIMENSIONS. Male : length 590–595μ ; breadth 365–370μ. Female ; length 710–740μ ; breadth 370–375μ.

HABITAT AND LOCALITY. Seven females and three males from bullock manure, Rothamsted Experimental Station, Harpenden, Herts. Holotype female, 1955.10.22.43 ; allotype male, 1955.10.22.44 and paratypes, 1955.10.22.45–52.

Macrocheles glaber (Müller)

Holostaspis glabra Müller, J. (1860). *K. K. mähr. schles. Ges. Brünn* : 178, figs.

Gamasus stercorarius Kramer, P. (1876). *Arch. Naturgesch.* **42** : 95, fig.

Holostaspis badius, Berlese, A. (1889). *Acari, Myriopoda etc.*, fasc. 52, N. 3.

Macrocheles marginatus var. *littoralis* Halbert, J. N. (1915). *Proc. Roy. Irish Acad.* **31**, 39 ii : 67, fig.

Macrocheles (*Copriholaspis*) *glaber* Berlese, A. (1921). *Redia* **14** : 85.

[1]*Macrocheles* (*Monoplites*) *oudemansii* Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9) **15** : 215. (in part)

Macrocheles veterrimus Sellnick, M. (1940). *Göteborg. Vetensk. Samh. Handl.* (5) 6B : 80, figs.

Copriholaspis anglicus Turk, F. A. (1946). *Ann. Mag. nat. Hist.* (11) **12** : 791, figs. *syn. nov.*

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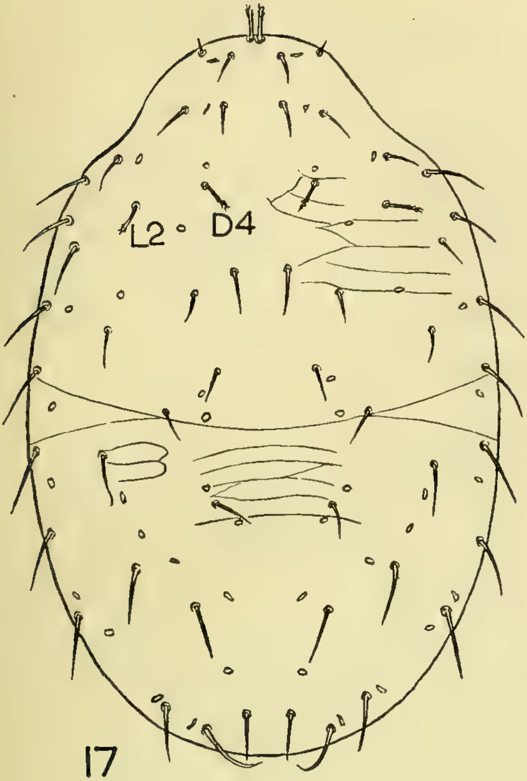
[1] Hull proposed this name for *Macrocheles marginatus* Oudemans, 1901 nec Herman, 1804. This "species," however, is a complex of at least two distinct species : the tritonymph being *M. glaber* and the adult, *M. plumiventris.*



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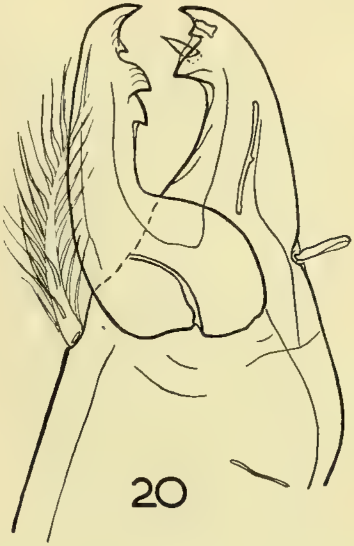

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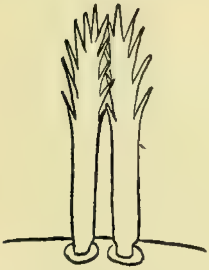

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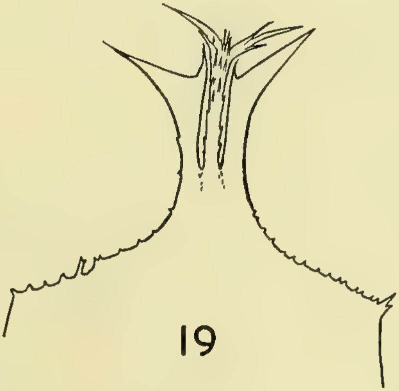

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FIGS. 17–20. *Macrocheles glaber* (Müller), female. Fig. 17, dorsal shield. Fig. 18, setae D1 enlarged. Fig. 19, tectum. Fig. 20, chelicera.

FEMALE. The dorsal shield is weakly reticulated and punctured, and carries twenty-eight pairs of setae and twenty-two pairs of " pores " (Text-fig. 17). The vertical setae, lying in close proximity to each other, are plumose in their distal half. Setae D8 are finely pilose, and D4 and L2 spiculate distally. The remainder of the setae on the shield are smooth and sharply pointed. The extra-marginal setae are simple and curved.

The tritosternum is normal. The sternal shield is characteristically ornamented with lines and punctate areas (Pl. 1, fig. 3). The transverse anterior, arcuate, transverse median and oblique lines are well defined. All the sternal setae are simple. The metasternal shields are small and the setae simple. The genital shield is strongly ornamented and provided with well-developed accessory sclerites. The ventri-anal shield (approx. 264–275μ long × 265–295μ wide) is ornamented with concentric punctate lines. The median pre-anal setae are situated well outside the connecting line between the anterior and posterior pre-anals. All the setae on the ventri-anal are simple. The metapodal shields are irregular in outline. The peritreme and peritrematal shield are normal for the genus.

The gnathosoma bears four pairs of setae ventrally. The internal posterior rostrals are about four times the length of the externals. The ventral groove has six transverse rows of denticles. The pedipalps are normal. The tectum is produced into three distinct processes ; the median being divided distally (Text-fig. 19). The chelicerae are strongly developed. The fixed digit is bidentate with the proximal tooth large and ridged (Text-fig. 20). The pilus dentilis is relatively short and stout. The movable digit is tridentate. The dorsal seta is comb-like distally.

Leg I (585μ) has plumed setae on the dorsal surface of the femur and genu. The tibia and tarsus are approximately equal in length (about 115μ). Legs II (510μ), III (460μ) and IV (760μ) have a few plumose setae on the femur and tarsus.

MALE. This sex is figured by Berlese (1889).

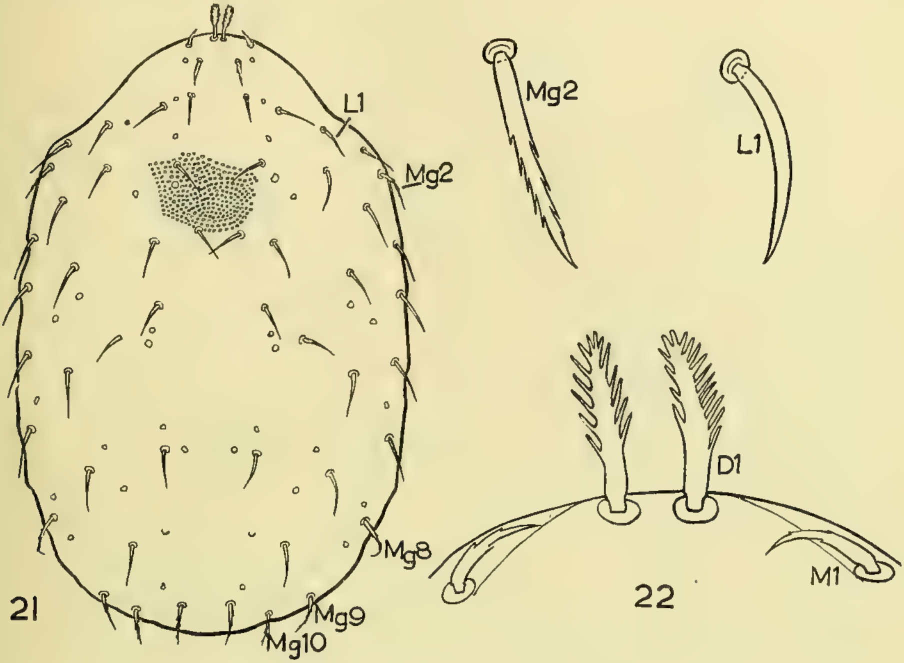
Dimensions. Female : length 850–855μ ; breadth 540–560μ.

HABITAT AND LOCALITY. This is one of the commonest species of mites found on " dor " beetles in Europe, especially on *Geotrupes stercorarius* Linn. It is also commonly encountered on Muscid flies.

Macrocheles punctoscutatus sp. nov.

FEMALE. Dorsal shield densely covered with minute punctures and bearing twenty-eight pairs of setae and twenty-two pairs of " pores " (Text-fig. 21). Vertical setae coarsely plumose, well separated (Text-fig. 22). The majority of dorsal setae smooth and sharply pointed apically ; setae D8, Mg2, Mg8–10 distinctly pilose. Extra-marginal setae simple.

Tritosternum normal, lacinae long and pilose. Sternal shield heavily ornamented, punctate areas conspicuous (Pl. 1, fig. 4). All sternal setae simple. Metasternal shields small, metasternal setae simple. Genital shield strongly ornamented, genital setae simple. Ventri-anal shield (320μ × 355μ) broader than long with its anterior margin lying in close proximity to the genital shield. The ornamentation of the shield consists of distinct lines forming a loose network, and numerous small punctures. The pre-anals, para-anals and post-anal seta are simple. The metapodals are small and elongate ; their long axis lying more or less parallel with that of the longer axis of the body.



FIGS. 21–22. *Macrocheles punctoscutatus* sp. nov., female. Fig. 21, dorsal shield. Fig. 22, setae D1 and M1 enlarged.

The external posterior rostral setae are about one-half the length of the internals. The ventral groove has five transverse rows of denticles. The dentition of the chelicerae and the structure of the tectum are similar to that in *M. glaber*.

Leg I (605μ) has the tibia and tarsus of about equal length.

DIMENSIONS. Length 880μ ; breadth 605μ.

HABITAT AND LOCALITY. A single female (holotype 1955.10.22.70) from a mole's nest at Churcham, Gloucestershire (Coll. R. S. George).

Macrocheles subbadius (Berl.)[1]

Holostaspis subbadius Berlese, A. (1904). *Redia* **1** : 264.

FEMALE. Dorsal shield bears twenty-eight pairs of setae and twenty-two pairs of " pores " (Text-fig. 23). The vertical setae are plumose distally. Setae D8 and, in the majority of the specimens examined, setae L2 are pilose. The extra-marginal setae are simple.

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[1] This species is figured by Berlese (1889) under *Holostaspis marginatus* (Herm.) Berl. " forma intermedia inter badium et adultum (marginatum) foem " in *Acari Myriopoda*, etc., fasc. 52, N. 6.

The sternal shield is ornamented with distinct punctures arranged as in Pl. 1, fig. 5. The sternal, metasternal and genital setae are simple. The ventri-anal shield (190–220 × 190μ) is ornamented with punctate lines ; the nine setae on this shield are simple. The metapodal shields are weakly sclerotized.

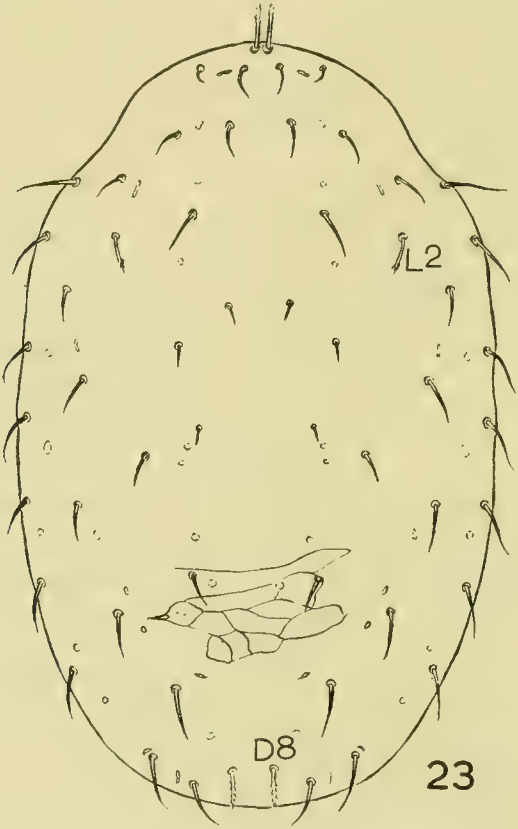


FIG. 23. *Macrocheles subbadius* (Berl.), female. Dorsal shield.

The lateral processes of the tectum are free and the form of the chelicerae is essentially the same as in *M. merdarius*.

Leg I has the tibia (82μ) shorter than the tarsus (110μ). The spines on tarsus II are short and stout.

MALE. Unknown.

DIMENSIONS. Length 610–625μ ; breadth 370–400μ.

HABITAT AND LOCALITY. Berlese (1889) records this species from manure in Italy. The writers have examined specimens from farmyard manure, Evesham, Worcestershire.

Macrocheles insignitus Berl.

Macrocheles (*Coprholaspis*) *insignitus* Berlese, A. (1918). *Redia* **13** : 158.

FEMALE. Dorsal shield with twenty-eight pairs of setae and twenty-two pairs of "pores". The surface of the shield is covered with minute punctures which form a polygonal network. All the setae on the shield and the interscutal membrane are simple. The verticals are short spine-like.

Sternal shield characteristically ornamented with punctures as in Pl. 1, fig. 6. All the sternal setae are simple. The metasternals are small and flank the anterior part of the ornamented genital shield. The metasternal and genital setae are simple. The ventri-anal shield is about as broad as long (156 × 152μ) and ornamented with punctate lines. The setae on this compound shield are all simple. The metapodals are extremely weakly sclerotised.

The gnathosoma is typical for the genus. The lateral processes of the tectum are free and fish-tail like ; the median process is strongly bifurcate distally. The form of the chelicerae is similar to that in *M. merdarius*.

Leg I (approx. 350μ in length) has the tibia (55μ) considerably shorter than the tarsus (72μ).

The male is unknown.

DIMENSIONS. Length 445μ ; breadth 275μ.

HABITAT AND LOCALITY. This species is previously known by a single female from the type locality "Longny, Orne in Gallia" (Berlese, 1918). The writers have examined a single female of this species from "a hot bed", Austrey, Warwickshire (undetermined in the Michael Collection).

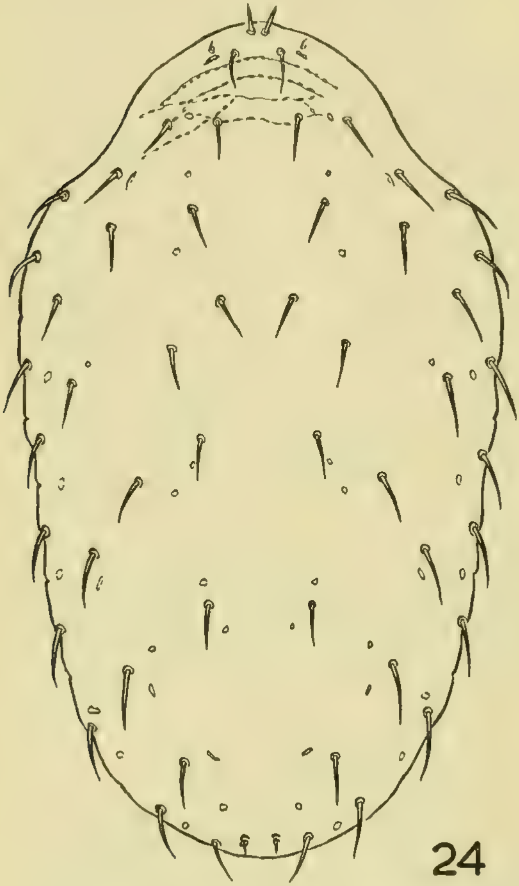
Macrocheles merdarius (Berl.)

Holostaspis merdarius Berlese, A. (1889). *Acari, Myriopoda et Scorpiones etc.*, Fasc. 52, N. 1, fig.
Macrocheles merdarius, Sellnick, M. (1940). *Göteborg. Vetensk. Samh. Handl.* (5) **6B** : 86, figs.

FEMALE. Dorsal shield, ornamented with reticulations, is provided with twenty-eight pairs of simple setae and twenty-two pairs of pores (Text-fig. 24). The vertical setae are sub-spinose. The extra-marginal setae are also simple.

The sternal shield is lightly ornamented with punctate lines and the three pairs of sternal setae are simple (Pl. 2, fig. 7). The metasternal shields are minute. Both the metasternal and genital setae are simple. The truncated anterior margin of the ventri-anal shield lies in close proximity to the posterior margin of the genital. The ventri-anal (about 150 × 126μ) is ornamented with four or five transverse lines. All the setae on this shield are simple. The metapodals are small and weakly sclerotized.

Ventral groove with five transverse rows of denticles. External posterior rostrals about one-third the length of the internals. The tectum has the lateral processes free (Text-fig. 25). The median process is deeply bifurcate. The dentition of the digits of the chelicerae is shown in Text-fig. 26.



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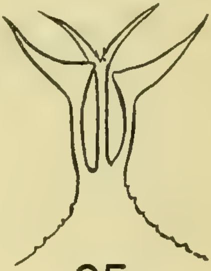

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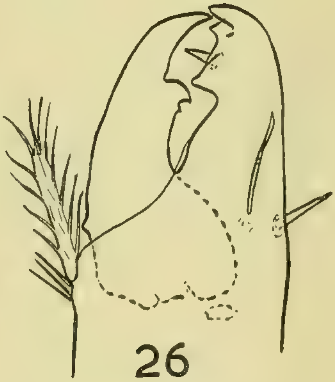

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FIGS. 24–26. *Macrocheles merdarius* (Berl.), female. Fig. 24, dorsal shield. Fig. 25. tectum. Fig. 26, chelicera.

MALE. This sex is described and figured by Berlese (1889).

DIMENSIONS. Female: length 445–490μ; breadth 225–280μ. Male: length 380μ; breadth not given by Berlese (1889).

HABITAT AND LOCALITY. This is one of the commonest species of Macrochelids occurring in dung and compost. It has been recorded from a number of localities in

Europe (Franz, 1954). In Britain it is recorded from bullock dung at Rothamsted Experimental Station, Harpenden, Herts. (Hyatt, 1956).

Macrocheles montanus (Willmann)

Nothrholaspis montana Willmann, C. (1951). *Bonner Zool. Beitr.* **2** : 158, figs.

FEMALE. Dorsal shield with twenty-nine pairs of setae and twenty-two pairs of "pores" (Text-fig. 27). The surface of the shield is conspicuously punctated and

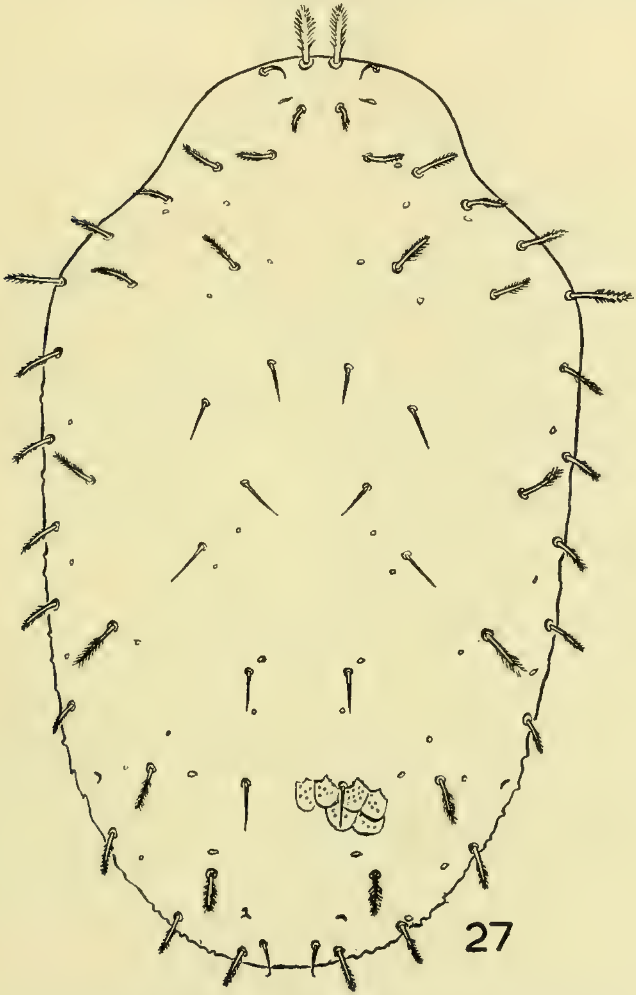

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FIG. 27. *Macrocheles montanus* (Willmann), female. Dorsal shield.

reticulated. Dorsal series (D) comprising nine pairs of setae. Vertical setae strongly plumose with their bases well separated. Setae M1, D5–D8, M3 and M4 and the additional setae of the D series are simple. The remainder of the dorsal setae are plumose. Extra-marginal setae are simple.

The sternal shield is covered with punctures which are larger in the posterior third of the shield (Pl. 2, fig. 8). The first pair of sternal setae are plumose in their distal third ; the second and third pairs are smooth or slightly plumose distally. The form of the metasternal and genital shield is shown in the figure. Ventri-anal shield (357 × 340μ) is ornamented with a network of punctate lines. The median pre-anal seta lies almost on the line connecting the anterior and posterior pre-anals. The pre-anal and para-anal setae are simple, the post-anal seta is strongly plumose distally. There are three pairs of platelets between the genital and ventri-anal shields. The metapodal shields are weakly sclerotized.

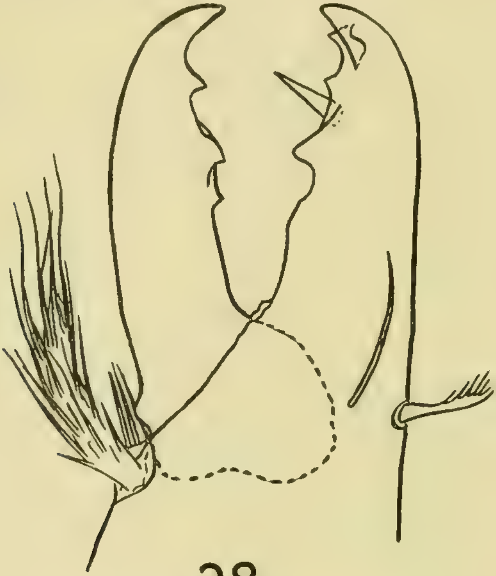

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FIG. 28. *Macrocheles montanus* (Willmann), female. Chelicera.

Venter of the gnathosoma normal for the genus. Tectum essentially the same as in *M. submotus* (Text-fig. 37). Both digits of the chelicerae tridentate (Text-fig. 28).

Leg I with the tarsus (175μ) longer than the tibia (154μ).

The male is unknown.

DIMENSIONS. Length 1,050–1,140μ ; breadth 660μ.

HABITAT AND LOCALITY. This species is previosuly known from Austria only

(Willmann, 1951 and Franz, 1954). We have examined a single female collected under "old wet oak bark" in Marley Wood, Wytham, Berkshire (Coll. E. W. Fager).

M. montanus is the only British species in the genus which has more than the normal compliment of setae on the dorsal shield. In Willmann's figure of the type specimen there are thirty-one pairs of setae on the shield; additional plumose setae being present near setae L7 and L9 as well as the simple pair in the D series. In other characters the British specimen agrees with the type.

Macrocheles carinatus (C. L. Koch).

Gamasus carinatus Koch, C. L. 1839. *Deutsch. Crust. Myr. Arach.* fasc. 24, t. 16.
Macrocheles hypochthonius Oudemans, A. C. 1913. *Ent. Ber. Amst.* **4** : 6.
Macrocheles hypochthonius Oudemans, A. C. 1914. *Arch. Naturgesch.* **79**A, Hft. 8 : 175, figs.
Nothrholaspis hulli Falconer, W. 1923. *Naturalist Lond.* : 153, figs. *syn. nov.*
Nothrholaspis carinata Sellnick, M. 1931. *SB. Akad. Wiss, Wien* **140** : 766, figs.

FEMALE. The dorsal shield is strongly reticulated and punctured, and its lateral margins serrated (Text-fig. 29). The vertical setae (D1) which stand in close proximity to each other, are long and strongly plumose in their distal half (Text-fig. 30). Setae M1 are short and may be smooth or plumose. Setae M3, M4, D6, D7, and D8 are thin and simple or slightly serrated distally. The remainder of the setae on the dorsal shield are strong and plumose. Setae D3 lie in advance of M2. The anterior extra-marginal setae are simple and the posterior plumose.

The sternal shield is ornamented with a network of ridges and punctures; the latter are especially large in the posterior third of the shield (Pl. 2, fig. 9). The sternal and metasternal setae are simple. The posterior margin of the genital shield is strongly convex, the genital setae are simple. The ventri-anal shield is sub-circular in outline and is strongly ornamented. All the setae on the compound shield are simple. The median pre-anals lie considerably closer to the anterior than the posterior pre-anals and are situated almost on the connecting line between these setae. The interscutal membrane between the genital and ventri-anal shield bears six platelets. The metapodal shields are small. The peritreme and peritrematal shield are normal for the genus. The interscutal membrane is conspicuously corrugated.

The external posterior rostral setae are about one-third the length of the internals. The ventral groove carries five rows of denticles. The tectum (Text-fig. 31) has the lateral lobes partially fused; the lateral and median lobes are divided distally. The chelicerae are strongly developed with the fixed digit tri-dentate (Text-fig. 32). The movable digit may be bi- or tri-dentate. The dorsal seta is serrated on one side.

Leg I, approximately 935μ in length, has the tibia (120μ) considerably shorter than the tarsus (165μ). Legs II, III, IV measure approximately 660μ, 605μ, and 1,100μ respectively.

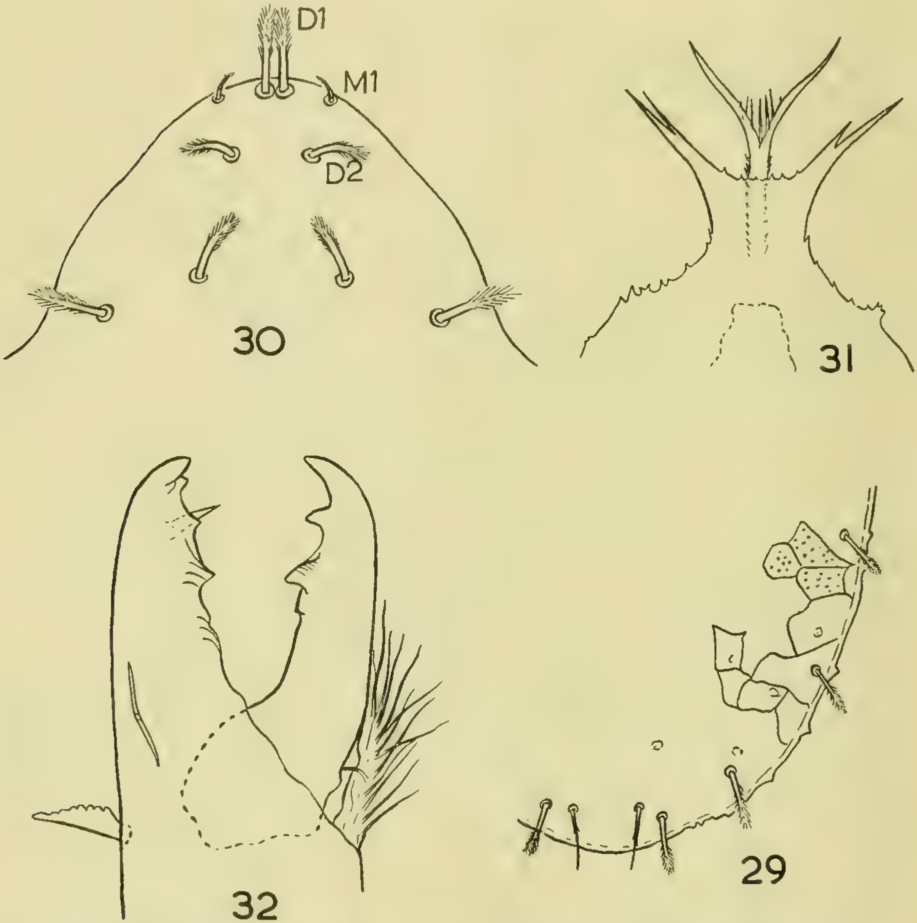
MALE. The chaetotaxy of the dorsal shield is basically the same as in the female. The sterniti-genital shield is provided with a polygonal network of ridges and strong punctures. The ventri-anal shield is also reticulated and punctured and measures about 298μ in length and 310μ in breadth. All the setae on this shield are simple.

The tectum is similar to that in the female. The spermatophoral process on the movable digit of the chelicera is short, being about one-half the length of the digit.

Femur, genu and tibia of leg II only are spurred.

Dimensions. Male: 880–900μ in length; 500–540μ in breadth. Female: 1,034–1,078μ in length; 570–640μ in breadth.

Habitat and locality. In humus and moss from a number of localities in the British Isles. This species has also been recorded from Austria, Germany and the Netherlands.

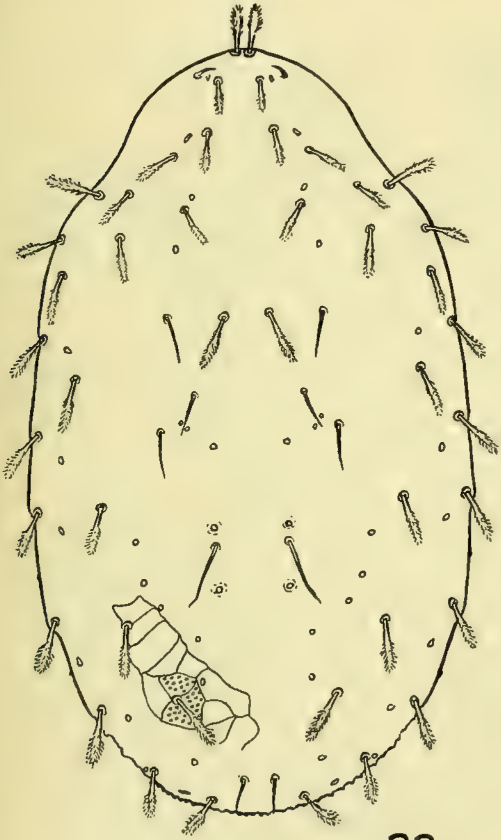


Figs. 29–32. *Macrocheles carinatus* (C. L. Koch), female. Fig. 29, postero-lateral margin of the dorsal shield. Fig. 30, anterior region of the dorsal shield. Fig. 31, tectum. Fig. 32, chelicera.

Macrocheles penicilliger Berl.

Holostaspis penicilliger Berlese, A. (1904). *Redia* **1** : 264.
Holostaspis penicilliger Berlese, A. (1918). *Redia* **13** : 146, 162.
Macrocheles penicilliger, Sellnick, M. (1940). *Göteborg. Vetensk. Samh. Handl.* (5) **6B** : 82, figs.

FEMALE. The dorsal shield is strongly reticulated and punctured, and has its lateral margins serrated (Text-fig. 33). Vertical setae, approximately 55μ in length, are plumose in their distal two-thirds. Their bases are almost contiguous. Setae M1, M3, M4, D6–D8 are simple ; remainder of dorsal setae plumose. Setae D8 are situated considerably anterior to the line connecting setae Mg10. Extra-marginal setae are plumose distally.



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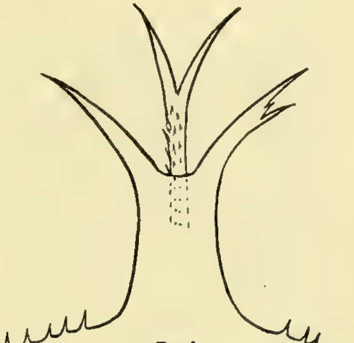

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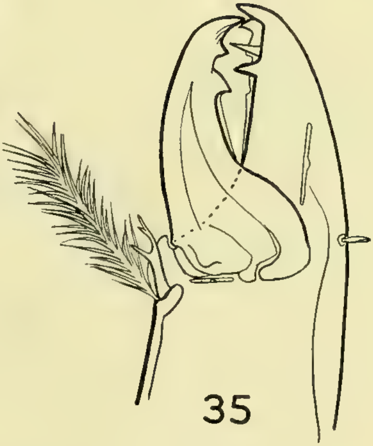

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FIGS. 33–35. *Macrocheles penicilliger* (Berl.), female. Fig. 33, dorsal shield. Fig. 34, tectum. Fig. 35, chelicera.

The sternal shield is heavily ornamented with ridges and punctures (Pl. 2, fig. 10) The first pair of sternal setae are strongly plumose and the second and third pair slightly plumose distally. The metasternal setae are simple as are the pair of setae situated on the punctured genital shield. On the ventri-anal shield (approx. 310 × 330μ), the pre-anal and para-anal setae are simple and the post-anal seta plumose. The median pre-anal lies outside the line connecting the anterior and posterior pre-anal. There are no platelets between the ventri-anal and genital shields. The metapodals are strongly sclerotized and elongate.

The external posterior rostrals on the venter of the gnathosoma are about one-third the length of the internals. Ventral groove has five transverse rows of denticles. The lateral processes of the tectum are partially fused ; distally these processes may or may not be divided (Text-fig. 34). The median process is deeply bifurcate. Both digits of the chelicerae are bidentate (Text-fig. 35). The pilus dentilis is short and thick at its base. The ventral seta is long and strongly pilose.

Leg I with tibia (approx. 99μ) considerably shorter than the tarsus (approx. 130μ).

MALE. Unknown.

DIMENSIONS. Female : length 900–930μ ; breadth 525–550μ.

HABITAT AND LOCALITY. This species has been found on *Trox scaber* (Linn.) in the nests of owls at Wytham, Oxford (Coll. C. E. Elton) and at Woodford, Essex (Coll. A. Hooper). Further records are from decaying leaves, Waterworks Valley, Jersey (Coll. G. Owen Evans), Italy (Berlese, 1904), Iceland (Sellnick, 1940) and Austria (Franz, 1954).

Macrocheles submotus Falconer,

Macrocheles cognatus Falconer, W. (1923). *Naturalist, Lond.* : 152, fig. (nom. praeocc.).

Macrocheles submotus Falconer, W. (1924). *Naturalist, Lond.* : 363 (nom. nov. pro. *M. cognatus*).

Macrocheles (*Nothrholaspis*) *occidentalis* Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9) **15** : 213, fig. syn. nov.

? *Macrocheles* (*Nothrholaspis*) *gloriosus* Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9) **15** : 214, fig. syn. nov.

FEMALE. Dorsal shield, strongly reticulated and punctured, is provided with twenty-eight pairs of setae and twenty-two pairs of pores. Its lateral margins are entire. Setae D1 plumose and situated about one diameter of their bases apart (Text-fig. 36). Setae M1, M4, D2, D5–D8, L1[1], Mg2 and Mg4 are simple, and Mg5 and Mg6 pilose. The remainder of the setae on the dorsal shield are distinctly plumose. The extra-marginal setae are simple or slightly pilose.

The tritosternum is normal with strongly pilose lacinae. The sternal shield, ornamented with strong ridges and large punctures, bears three pairs of simple, spine-like setae (Pl. 2, fig. 11). The metasternal and genital setae are also simple. Ventri-anal shield (approx. 450 × 430μ) is triangular in outline and ornamented with ridges and punctures. The pre-anal and para-anal setae are simple. The median pre-anal lies outside the line connecting the anterior and posterior pre-anals. Three pairs of platelets lie between the ventri-anal and genital shields. The interscutal membrane is closely striated. The peritreme and peritrematal shields are normal.

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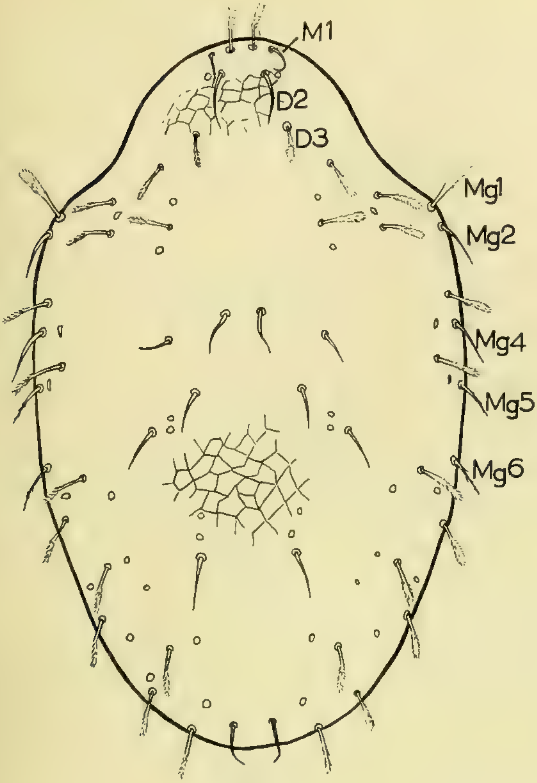
[1] This seta should be simple in Text-fig. 36.


M1
D2
D3
Mg1
Mg2
Mg4
Mg5
Mg6

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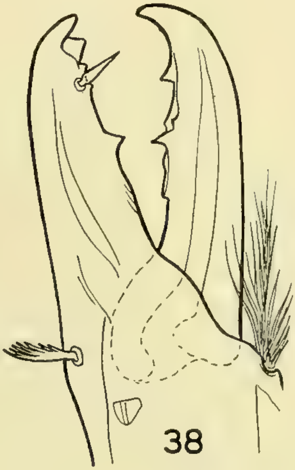

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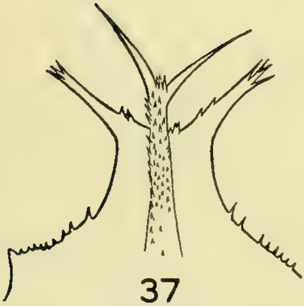

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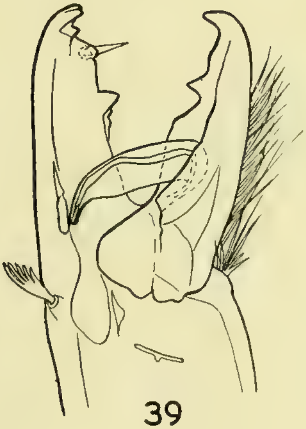

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Figs. 36–39. *Macrocheles submotus* Falconer. Fig. 36, dorsal shield of female. Fig. 37, tectum of female. Fig. 38, chelicera of female. Fig. 39, chelicera of male.

The external posterior rostrals on the venter of the gnathosoma are about one-half the length of the internals. The ventral groove carries five transverse rows of denticles The form of the tectum is shown in Text-fig. 37. Both digits of the chelicerae are massive (Text-fig. 38). The fixed digit has two strong and two weaker teeth ; the movable digit is basically bi-dentate. The dorsal seta is comb-like.

Leg I (approx. 1,100μ in length) has the tibia (205μ) shorter than the tarsus (220μ). Legs II–IV measure respectively about 1,150μ, 1,078μ and 1,700μ.

MALE. The chaetotaxy and ornamentation of the dorsal shield is essentially the same as in the female. Ventrally, the truncated sterniti-genital shield is coarsely punctured. The five pairs of setae on this compound shield are simple. The ventri-anal shield (350 × 340μ) is reticulated and punctured ; there are no platelets between the ventri-anal and genital shield. Both digits of the chelicerae are dentate as in Text-fig. 39. The spermatophoral process is considerably shorter than the length of the digit.

The femur, genu and tibia of leg II only are spurred.

DIMENSIONS. Male : length 1,050–1,100μ ; breadth 620–630μ. Female : 1,390–1,450μ ; breadth 780–820μ.

HABITAT AND LOCALITY. This is one of the commonest, and most widely distributed Macrochelid found in litter and humus under deciduous and coniferous trees in Britain.

The above description of *submotus* is based on specimens compared with the type in the Falconer Collection at the Liverpool Museum. This species has also appeared under the name of *Macrocheles tridentinus* (Can.) in British and possibly other European faunal lists. The original description of *tridentinus* was based on the male only and both description and drawings are insufficient for the certain identity of the species. Canestrini gives the length of the male of *tridentinus* as 860μ.

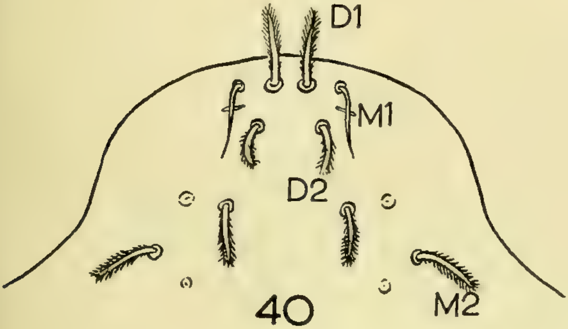
Macrocheles tardus (C. L. Koch)

Gamasus tardus Koch, C. L. 1841. *Deutsch. Crust. Myr. Arach.* fasc. 39, t. 14.
Nothrholaspis tardus, Sellnick, M. 1931. *S.B. Akad. Wiss. Wien.* **140** : 765, figs.

FEMALE. Dorsal shield, strongly reticulated and punctured, is provided with twenty-eight pairs of setae and twenty-two pairs of pores. The vertical setae (D1) are plumose and well separated, setae M1 are long, simple and extend beyond the bases of D2 by about one-half their length (Text-fig. 40). Setae M3, M4, D6 and D8 are simple, D7 are finely pectinated whilst the remainder of the setae of the dorsal shield are strongly plumose. The marginal setae (Mg) are situated a short distance from the lateral margin of the shield (Text-fig. 41). The anterior extra-marginal setae are pectinate and the posterior extra-marginals plumose.

The tritosternum is normal with strongly pilose lacinae. The sternal shield is ornamented with a polygonal network of ridges and numerous punctures (Pl. 2, fig. 12). All the sternal setae are simple. The metasternal shields are small and the setae plumose. The strongly punctured genital shield is convex posteriorly and bears a pair of simple setae. The ventri-anal shield, about as broad as long (330 × 300μ) is reticulated and punctured. The anterior and posterior pre-anals are simple but the median pre-anal may be simple or pectinate. The para-anals are long and simple and the post-anal seta short and plumose. The region between the genital and ventri-anal shields is usually provided with three pairs of platelets. This number may be reduced in some specimens. The metapodal shields are small. The peritreme and peritrematal shield are normal. The interscutal membrane is coarsely striated, the striae being provided with triangular processes at intervals along their length.

Ventrally, the gnathosoma has the normal four pairs of setae of which the external posterior rostrals are about one-half the length of the internals. The ventral groove



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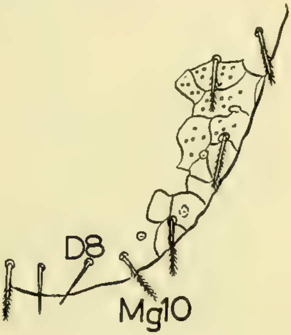

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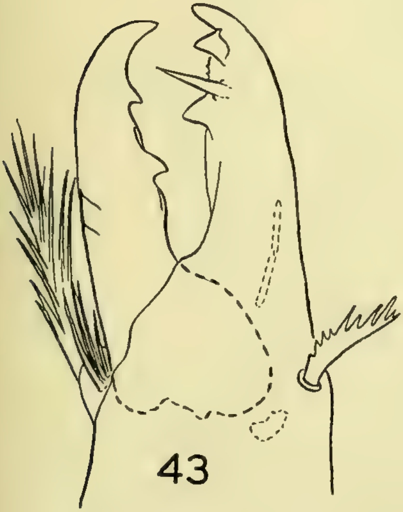

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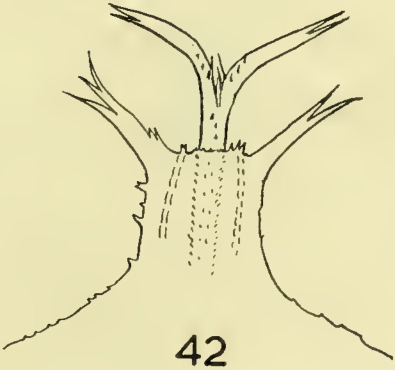

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FIGS. 40–43. *Macrocheles tardus* (C. L. Koch), female. Fig. 40, anterior region of the dorsal shield. Fig. 41, postero-lateral margin of dorsal shield. Fig. 42, tectum. Fig. 43, chelicera.

has five rows of denticles. The lateral processes of the tectum are partially fused (Text-fig. 42); the distal end of these processes being bi- or trifurcate. The stout median process is divided; each arm being entire or divided distally. The fixed digit of the chelicera is provided with two strong teeth and between them two or three weaker teeth (Text-fig. 43). The pilus dentilis is long and stout. The movable digit has two recurved teeth only. The dorsal seta is large and comb-like.

Leg I (approximately 1,020μ in length) bears plumose setae on the femur, genu and tibia. The tibia (165–175μ) is shorter than the tarsus (200–215μ). Leg II (880μ) has plumose setae on the trochanter and tarsus as have leg III (820μ) and leg IV 1,485μ).

MALE. The chaetotaxy and ornamentation of the dorsal shield is essentially the same as in the female. The sterniti-genital shield, truncated posteriorly, is heavily reticulated and punctured. The five pairs of setae on the compound shield are simple. The ventri-anal shield (330 × 350μ) is also reticulated and punctured. The pre-anal and para-anal setae are usually simple, but may be pectinate. The post-anal seta is strongly pilose. The chelicerae are basically the same as in *M. cognatus*, differing only in the position of the large proximal tooth on the fixed digit. The spermatophoral process is considerably shorter than the length of the movable digit. The femur, genu and tibia of leg II are the only segments which are spurred.

DIMENSIONS. Male: 1,030–1,100μ in length; 627–700μ in breadth. Female 1,215–1,290μ in length; 730–800μ in breadth.

HABITAT AND LOCALITY. In vegetable debris near Rydal Water, Westmorland and in decaying leaves, Waterworks Valley, Jersey. This species has also been recorded from a number of other localities in Europe (Franz, 1954).

Macrocheles decoloratus (C. L. Koch)

Gamasus decoloratus Koch, C. L. (1893). *Deutsch. Crust. Myr. Arach.* fasc. 25, t. 14.
Macrocheles decoloratus, Oudemans, A. C. (1913). *Ent. Ber. Amst.* **4**: 5.
Macrocheles decoloratus, Oudemans, A. C. (1914). *Arch. Naturgesch.* **79A** Hft. 8: 173.

FEMALE. Dorsal shield, weakly reticulated but strongly punctured, bears twenty-eight pairs of setae and twenty-two pairs of pores (Text-fig. 44). The vertical setae (D1) are well separated and strongly plumose. The remainder of the setae on the dorsal shield are also plumose. A characteristic feature of the chaetotaxy is the relative length of setae Mg9 and 10. The latter is approximately equal in length to D8, but only about one-half the length of Mg9. The extra-marginal setae are plumose.

The tritosternum is normal. The sternal shield (195μ long × 220μ wide) is ornamented with a faint reticulate pattern and large punctures (Pl. 3, fig. 13). The punctate areas are usually conspicuous. The three pairs of sternal setae and the metasternals are long and simple or slightly pectinate. The genital shield is strongly punctured and has a network of punctate lines in its anterior half. The genital setae usually are simple. The ventri-anal shield (286–298μ long × 250–286μ wide) is provided with a network of punctate lines. The lateral regions of the shield are densely punctured. The pre-anal and para-anal setae are long and simple. The post-anal seta is shorter and plumose. There are no platelets between the genital and ventri-anal shield. The metapodals are small and irregular in outline. The peritreme and peritrematal shields are normal.

Ventrally, the gnathosoma carries the normal four pairs of setae. The external posterior rostrals are about one-third the length of the internals. The capitular groove is provided with five transverse rows of denticles. The tectum (Text-fig. 45) has the three anterior processes separate. The movable digit of the chelicera is tridentate and the fixed bi- or tridentate (Text-fig. 46). The dorsal seta is spatulate.

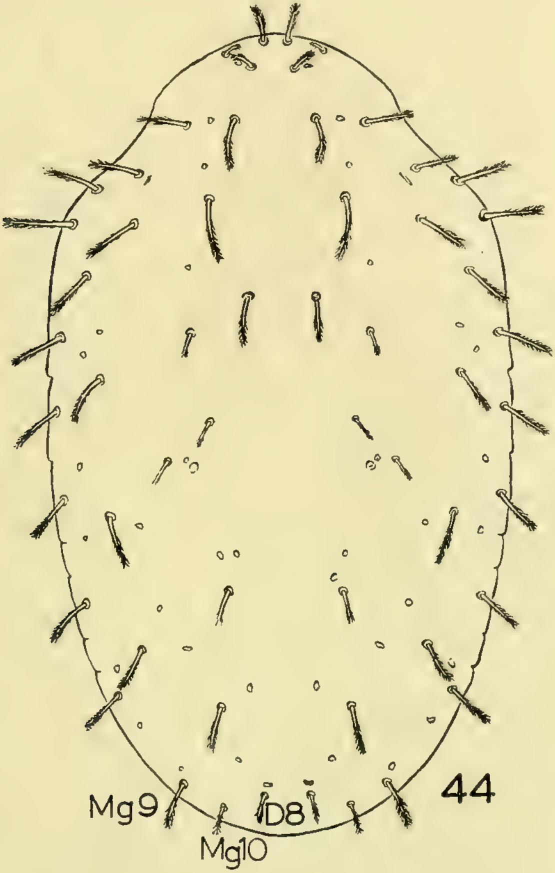


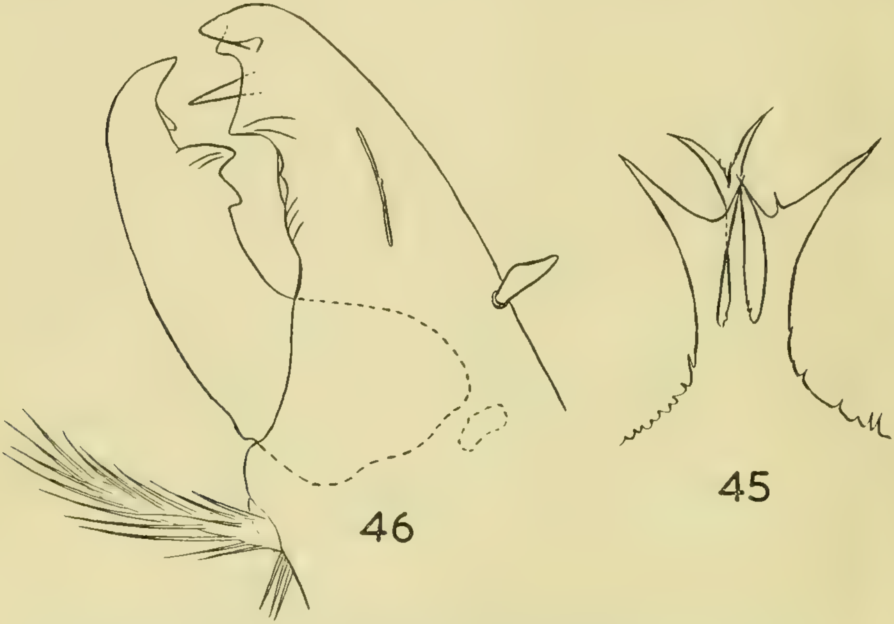
FIG. 44. *Macrocheles decoloratus* (C. L. Koch), female. Dorsal shield.

Leg I (approx. 670μ) with plumose setae on femur, genu and tibia. Tarsus I (132–140μ) longer than tibia I (121μ). Leg II (680μ). Leg III (638μ) and Leg IV (990μ) with some plumose setae on trochanter and tarsus.

MALE. Unknown.

DIMENSIONS. Length 850–880μ; breadth 510–520μ.

HABITAT AND LOCALITY. In cow dung, nr. Canterbury, Kent (Coll. E. Warren, 1942). This species has also been recorded from Austria, Germany and the Netherlands.



FIGS. 45—46. *Macrocheles decoloratus* (C. L. Koch), female. Fig. 45, tectum. Fig. 46, chelicera.

Macrocheles matrius (Hull).

Nothrholaspis matrius Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9) **15** : 212.

Macrocheles subbadius var. *robustulus*, Sellnick, M. (1940). *Göteborg. Vetensk. Samh. Handl.* (5) **6B** : 86, figs.

Macrocheles carinatus, Hughes, A. M. (1948). *Mites associated with stored food products.* H.M.S.O. : 126, figs.

FEMALE. Superficially, the chaetotaxy of the dorsal shield in this species resembles that in *M. decoloratus*. The chief difference between the species lies in the relative lengths of setae Mg9 and Mg10 which in the present species are approximately equal in length (Text-fig. 47). The extra-marginal setae are slightly plumose.

The sternal shield (187μ long × 220μ wide) has well developed lines and a few punctures (Pl. 3, fig. 14). The punctate areas are considerably larger and more strongly developed than in *M. decoloratus*. The sternal and metasternal setae are simple or slightly pectinate. The genital shield is ornamented with punctate lines and large punctures. The genital setae are plumose distally. The ventri-anal shield

(340μ × 375μ wide) is characteristically ornamented. The pre-anal and para-anal setae are simple. The post-anal seta is short and plumose distally. Metapodals are elongate and weakly sclerotized.

The gnathosoma is essentially the same as in *decoloratus* except for the structure of the tectum; in *matrius* the external margin of the lateral processes are strongly serrulate (Text-fig. 48).

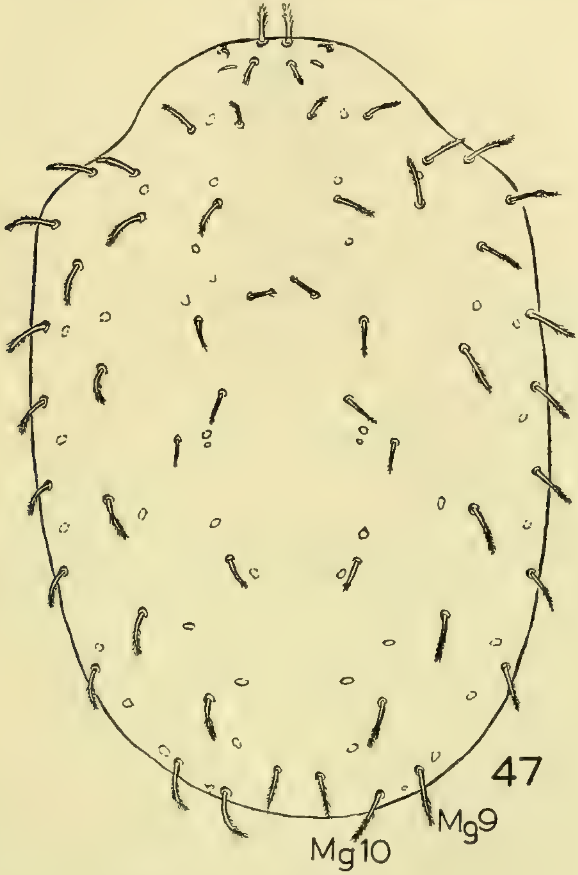


FIG. 47. *Macrocheles matrius* Hull, female. Dorsal shield.

MALE. This sex is adequately described and figured by Hughes (1948).

DIMENSIONS. Male: length 680–720μ; breadth not stated by Hughes (1948). Female: length 890–910μ; breadth 540–565μ.

HABITAT AND LOCALITY. Hull (1925) states that the species is " not uncommon in north of England. Abundant in poultry manure, West Allendale ". We have examined specimens from the nest of *Riparia riparia* at Tirley, Gloucestershire (Coll. R S. George) and from poultry manure at Houghton, Huntingdonshire (Coll. C. Horton Smith). Hughes (1948) records it under the name *M. carinatus* from floor debris and sievings of grain.

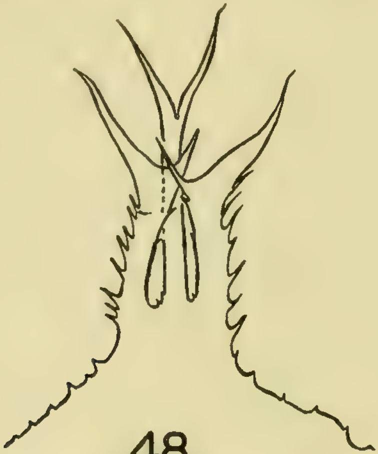


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FIG. 48. *Macrocheles matrius* Hull, female. Tectum.

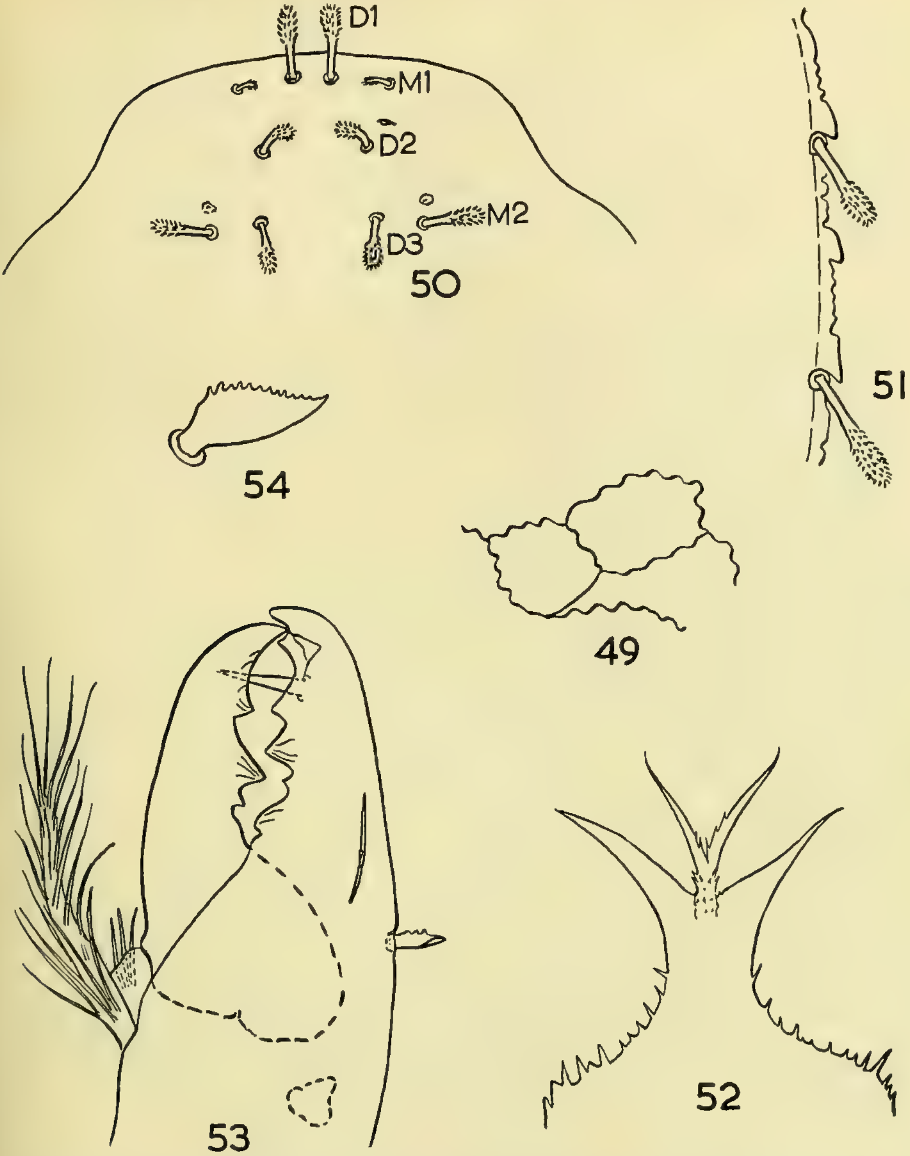
M. matrius is undoubtedly conspecific with *Macrocheles subbadius* var. *robustulus* (Berl.) Sellnick (1940). If the species described and figured by Sellnick is the same as *robustulus*, there is some doubt concerning this, then *matrius* must be considered a synonym.

Macrocheles pluiventris Hull

Holostaspis marginatus Berlese, A. (1889). *Acari, Myriopoda et Scorpiones, etc.*, fasc. 52, No. 4 and 5, figs.
? *Macrocheles gladiator* Hull, J. E. (1918). *Trans. Nat. Soc. Northumb.*, N.S. **5** : 71, figs.
? *Macrocheles plumipes* Hull, J. E. (1918). tom. cit. : 72, fig.
Macrocheles (Monoplites) oudemansii Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9), **15** : 215 (in part).
Macrocheles plumiventris Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9), **15** : 216, figs.
Nothrholaspis fimicola Sellnick, M. (1931). *S.B. Akad. Wiss. Wien* **140** : 765, fig. *syn. nov.*

FEMALE. The dorsal shield is strongly reticulated, especially in its posterior two-thirds. The lines of the mesh-work are distinctly crenulated (Text-fig. 49). The vertical setae (D1) which are well separated, and setae D2–D4, M2, series L and series Mg. are strongly plumose in their distal half (Text-fig. 50). Setae M1 are short and relatively weakly plumose ; setae D6–D8 and Mg2–3 are considerably finer and less plumose than the L and the remainder of the Mg. series. The marginal setae are situated on the serrated lateral margin of the dorsal shield (Text-fig. 51). The extra-marginal setae are plumose.

The tritosternum is normal. All the ventral shields are strongly reticulated and



FIGS. 49–54. *Macrocheles plumiventris* Hull, female. Fig. 49, ornamentation of the dorsal shield. Fig. 50, anterior region of the dorsal shield. Fig. 51, lateral margin of the dorsal shield. Fig. 52, tectum. Fig. 53, chelicera. Fig. 54, dorsal seta on chelicera

punctured (Pl. 3, fig. 15). The sternal shield bears three pairs of sternal setae of which h1 is strongly plumose and h2–3 smooth and blunt. The metasternal shields are free and the setae plumose. The genital shield is provided with accessory sclerites and the genital setae are plumose. The ventri-anal shield is considerably broader than long (370–460μ × 490 610μ) and characteristically shaped. The three pairs of pre-anal setae are plumose, the para-anal setae fine and slightly pilose, and the post-anal seta short and strongly plumose. The metapodal shields are well developed. The peritreme and peritrematal shield are normal for the genus.

Ventrally, the gnathosoma bears four pairs of setae. The external posterior rostrals are more than one-half the length of the internal posterior rostrals. The ventral groove is provided with seven rows of denticles. The pedipalps are normal. The tectum has its lateral processes partially fused. The apex of these processes may be entire or bifurcated (Text-fig. 52). The median process is strongly bifid distally. The fixed digit of the chelicera has five teeth of which the larger are ridged (Text-fig. 53). The movable digit is provided with three teeth, the proximal being the smallest. The dorsal seta has a denticulate margin (Text-fig. 54). The ventral setae are long and strongly pilose.

Leg I, about 1,200μ in length, has plumose setae on the femur, genu and tibia. Trochanter I bears a short conical spur internally. Tibia I measures 220–242μ and Tarsus I 210–220μ. Leg II is stout, approximately 1,100μ in length and richly provided with plumose setae as are leg III (approx. 1,030μ) and Leg IV (approx. 1,650μ.). The pulvilli and claws of Legs II–III are well developed.

MALE. The ornamentation and chaetotaxy of the dorsal shield is basically the same as in the female. The venter is covered by a reticulated holoventral shield. The fixed digit of the chelicera is provided with four teeth in its distal half. The movable digit, in the specimen under study, has a single tooth. Berlese (1889) shows four teeth on this digit ! The spermatophoral process is longer than the movable digit and is pointed distally. The trochanter, femur, genu, tibia and tarsus of Leg II are provided with spurs, also genu III, and trochanter and femur IV.

DIMENSIONS. Male : 913μ in length and 605μ in breadth (a single specimen in the Michael Collection). *Female* : 1,150–1,480μ in length and 750–935μ in breadth.

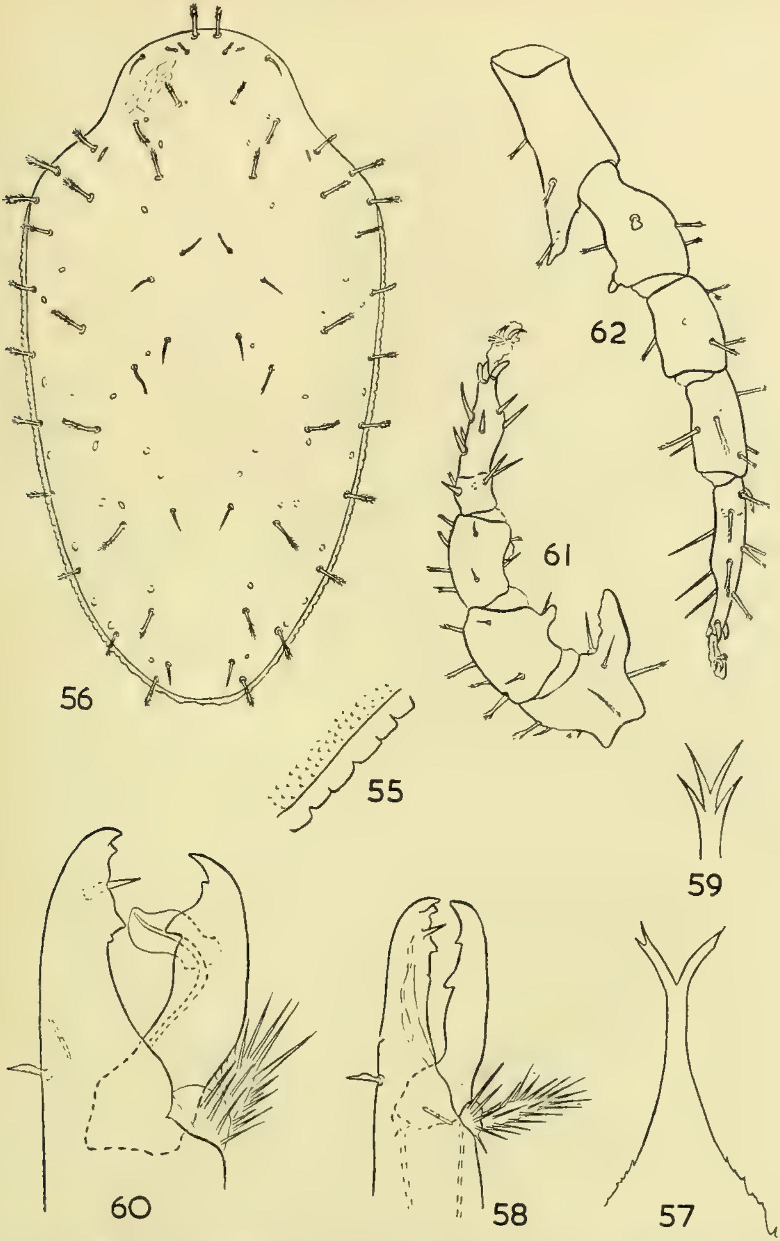
HABITAT AND LOCALITY. In manure and compost heaps. Common and widely distributed in Europe.

Sellnick (1931) drew attention to the fact that *Holostaspis marginatus* Berl. (1889) was not *Acarus marginatus* Hermann (1804) and proposed the name *Nothrholaspis fimicola* for Berlese's species. Hull (1925) had, however, already described this species under *Macrocheles plumiventris*. It is also possible that Hull's *Macrocheles gladiator* and *plumipes* are referable to this species, but the original descriptions and figures are wholly inadequate for their certain identity.

Macrocheles superbus **Hull**

Macrocheles superbus Hull, J. E. (1918). *Trans. Nat. Hist. Soc. Northumb.*, N.S. **5** : 71, figs.

FEMALE. Dorsal shield minutely punctured and with a faint reticulated pattern in its posterior half. The lateral margin of the shield is evenly serrated (Text-fig. 55).



FIGS. 55–62. *Macrocheles superbus* Hull. Fig. 55, lateral margin of dorsal shield. Fig. 56, dorsal shield of female. Fig. 57, tectum of female. Fig. 58, chelicera of female. Fig. 59, distal end of tectum of male. Fig. 60, chelicera of male. Fig. 61, leg II of male. Fig. 62, leg IV of male.

The vertical setae (D1) are stout, plumose and widely separated (Text-fig. 56). Setae D4–D8, M3 and M4 are simple and minutely spiculate distally. The remainder of the dorsal setae are stout and plumose. The extra-marginal setae are plumose distally.

The tritosternum is normal with the lacinae strongly pilose. The sternal shield is ornamented with a network of ridges and punctures (Pl. 3, fig. 16). The punctate areas are distinct. The first pair of sternal setae (h1) are strongly plumose whereas h2 and h3 are simple and blunt apically. The metasternal setae are similar in form to setae h2 and h3. The genital shield, strongly punctured, is provided with accessory sclerites and a pair of rod-like setae which are spiculate dorsally. The ventri-anal shield (approximately 580 × 460μ) is strongly reticulated and punctured. The anterior pre-anal setae are simple and the median and posterior setae plumose. The para-anals are simple and the post-anal plumose. A pair of well-sclerotized platelets lie between the genital and ventri-anal shields. The metapodal shields are well developed. The peritreme and peritrematal shield are normal.

The four pairs of ventral setae on the gnathosoma are simple with the external posterior rostrals about one-eighth the length of the internals. The former lie well in advance of the latter. The ventral groove is provided with five rows of denticles. The tectum consists of a single process, bifurcate distally (Text-fig. 57). The chelicerae are strongly chelate-dentate with the fixed digit bearing two well-developed teeth and a strong *pilus dentilis* (Text-fig. 58). The movable digit is also bidentate.

Leg I (approx. 480μ) with the tibia (230–240μ) considerably shorter than the tarsus (297–320μ).

MALE. The chaetotaxy and ornamentation of the dorsal shield is essentially the same as in the female except for a characteristic densely punctured area surrounding the base of setae L6. In the majority of the males examined the dorsal shield was strongly attentuated in the posterior third.

The sterniti-genital shield is poorly ornamented with a network of ridges and punctures and its posterior margin is slightly concave. The five pairs of setae on the shield are all plumose distally. The ventri-anal shield (approximately 560 × 350μ) is provided with a polygonal network of ridges and numerous punctations. The pre-anal setae and the post-anal seta are plumose in their distal half. The para-anals are simple. The interscutal membrane between the sterniti-genital and ventri-anal shield is without sclerotized platelets. The metapodal shields are well developed.

The structure of the venter of the gnathosoma is basically the same as in the female. The tectum may be bifurcate or more extensively divided distally (Text-fig. 59). The fixed digit of the chelicera is tridentate and the movable bidentate. The spermatophoral process is about one-third the length of the movable digit (Text-fig. 60).

Femur, genu and tibia of leg II (Text-fig. 61) and the trochanter and femur of leg IV (Text-fig. 62) are spurred.

DIMENSIONS. Male: 1,420–1,520μ in length, 850–900μ in breadth. Female: 1450–1650μ in length, 790–900μ in breadth.

HABITAT AND DISTRIBUTION. Common in wrack and tidal debris above high-water mark on the seashore. Also recorded from salt marshes (Falconer, 1923). Widely distributed in Britain.

SPECIES INCERTAE SEDIS

Macrocheles (Nothrholaspis) pannosus Hull

Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9), **15** : 211, fig.

It is possible that this species is a small form of *M. plumiventris.*
DIMENSIONS. Female : 900μ in length.
HABITAT AND LOCALITY. " In manure, West Allendale."

Macrocheles (Nothrholaspis) nemoralis Hull

Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9), **15** : 213, fig.

This species is possibly a synonym of *M. penicilliger.*
DIMENSIONS. Female : 810μ in length, 500μ in breadth.
HABITAT AND LOCALITY. " West Allendale ; habitat unknown."

Macrocheles (Nothrholaspis) parmulatus Hull

Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9), **15** : 214, fig.

DIMENSIONS. Female : 1,200μ in length.
HABITAT AND LOCALITY. " West Allendale ; habitat unknown."

Macrocheles (Monoplites) palustris Hull

Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9), **15** : 216, fig.

DIMENSIONS. Male : 1,100μ ; female, 1,200μ.
HABITAT AND LOCALITY. " In sphagnum on the moors, West Allendale."

Macrocheles (Monoplites) tardior Hull

Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9), **15** : 216, fig.

DIMENSIONS. Female : 1,000μ in length.
HABITAT AND LOCALITY. " Oxfordshire (R. S. Bagnall). Habitat not stated."

Genus ***GEHOLASPIS*** Berl. s. lat.

Geholaspis Berlese, A. (1918). *Redia,* **13** : 145.

This genus has been revised by Valle (1953) and may be defined as follows :

Dorsal shield with twenty-eight pairs of setae and twenty-two pairs of " pores ". Sternal shield with three pairs of setae ; metasternal shields free or fused with the endopodal shields. Ventri-anal shield in the female with *five* pairs of pre-anal setae. Chelicerae normal length with a few teeth or conspicuously elongate and multidentate Tectum with median process only. Other characters as in *Macrocheles* Latr.

TYPE : *Gamasus longispinosus* Kramer, 1876.

Valle (loc. cit.) subdivided the genus into three subgenera of which the following two are represented in the British fauna :

1. Seta M1 long and simple, and extending beyond the bases of D2 by more than half their length (fig. 63). Ratio of the length of the dorsal shield to the length of the movable digit of the chelicera varies between 6·8 and 10·4 ; movable digit with less than 5 teeth . . . . *Geholaspis* s. str.

Seta M1 short, simple or plumose, and not or scarcely extending beyond the bases of seta D2 (fig. 66). Ratio of the length of the dorsal shield to the length of the movable digit of the chelicera varies between 3·7 and 4·5 ; movable digit with more than five teeth . . . . *Longicheles* Valle.

The subgenus *Geholaspis* is represented in Britain by the type species only, and *Longicheles* by two species, namely, *G.* (*L.*) *mandibularis* (Berl.) and *G.* (*L.*) *longulus* (Berl.).

Subgenus ***GEHOLASPIS*** Berl. s. str.

Geholaspis (Geholaspis) longispinosus (Kramer).

Gamasus longispinosus Kramer, P. (1876). *Arch. Naturgesch.* **42** : 100, fig.
Holostaspis longispinosus, Berlese, A. (1887). *Acari, Myriapoda et Scorpiones, etc.*, fasc. **44**, No. 1, figs.
? *Macrocheles castaneus* Hull, J. E. (1925). *Ann. Mag. nat. Hist.* (9), **15** : 212.

FEMALE. The dorsal shield is minutely punctured all over and reticulated in its posterior half. It carries twenty-eight pairs of setae and twenty-two pairs of " pores " distributed as in Text-fig. 63. Setae D1 are strongly plumose ; D2, D5–D8, M1, M5 and M6, and L1 are simple. The remainder of the dorsal setae are pilose. The extra-marginal setae are similar in structure to the marginal series.

The tritosternum is normal with the lacinae pilose. The sternal shield is ornamented with a network of ridges and punctures (Pl. 4, fig. 17). The three pairs of sternal setae and the metasternals are simple. The genital shield is broad and strongly sculptured. The genital setae are simple and the accessory sclerites well-developed. The large ventri-anal shield (440–440μ in length and 465–510μ in breadth) is broader than long and bears five pairs of pre-anal setae in addition to the three setae normally associated with the anus. The relative lengths of these setae are shown in Text-fig. 4. The surface of the shield is evenly reticulated. The metapodal shields are small and weakly sclerotized. The peritrematal shield is free in its posterior half.

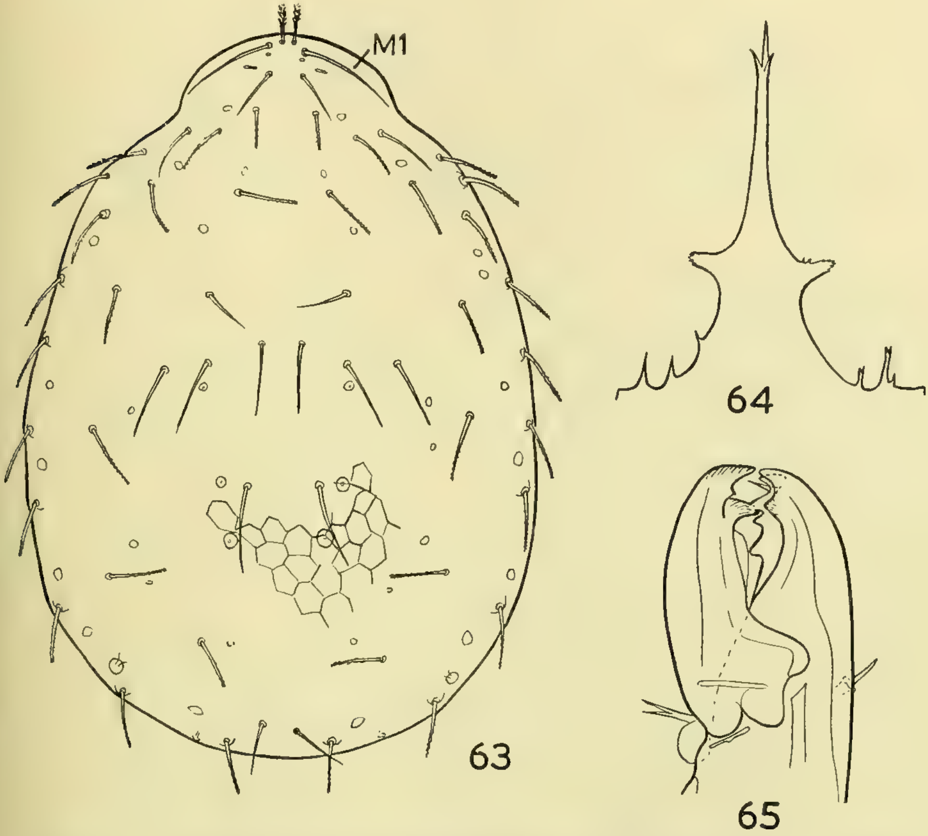
Ventrally, the gnathosoma bears the normal four pairs of setae. The external posterior rostrals lie well in advance of the internals. The ventral groove is provided with six transverse rows of denticles. The corniculi are long and slender. The tectum comprises a median process arising from a denticulate base (Text-fig. 64). The process is provided with shoulder-like projections of varying size and shape about a third of the distance from its base ; distally it is divided into two or three pointed branches.

The chelicerae are strongly developed and dentate; the dentition of the digits is shown in Text-fig. 65. The ventral setae, omitted from the figure, are well developed.

Tibia I (approx. 84μ) is considerably shorter than tarsus I (approx. 133μ).

Male. This sex does not appear to have been described.

Dimensions. Length, 870–970μ; breadth 590–710μ.



Figs. 63–65. *Geholaspis* (*Geholaspis*) *longispinosus* (Kramer), female. Fig. 63, dorsal shield. Fig. 64, tectum. Fig. 65, chelicera.

Habitat and locality. This species is widely distributed in Europe (Valle, 1953) and relatively common in moss, litter and humus. It has been recorded from North Wales by Hull (1918) and from Ireland by Halbert (1915). The writers have examined specimens from a number of localities in England, Wales and Scotland.

The figures of the dorsal and ventri-anal shields of *Geholaspis longispinosus* (Kramer) given by Valle (1953, figs. I and V (2)) do not appear to refer to this species but to *Geholaspis forolivensis* Lombardini, 1943, which he considers to be a subspecies of *longispinosus*. In *forolivensis* the lateral and marginal series of dorsal setae are strongly plumose as in *mandibularis*, and the shape of the ventri-anal shield and the relative lengths of the pre-anal setae do not conform with those in *longispinosus*.

Subgenus ***LONGICHELES*** Valle

The two British species of this subgenus may be separated as follows :

1. Setae M1 simple ; a simple seta situated between plumose setae L3 and L4 ; dorsal shield less than 650μ in length . . . . . . *G.(L.) longulus* (Berl.)

–. Setae M1 strongly plumose ; without simple seta between plumose setae L3 and L4 (Text-fig. 66) ; dorsal shield about 750μ in length . . *G.(L.) mandibularis* (Berl.)

Geholaspis (Longicheles) longulus (Berl.)

Holostaspis longulus Berlese, A. (1887). *Acari, Myriapoda et Scorpiones, etc.*, fasc. 43, no. 9, figs.
Geholaspis (*Longicheles*) *longulus*, Valle, A. (1953). *Redia* **38** : 351, figs.

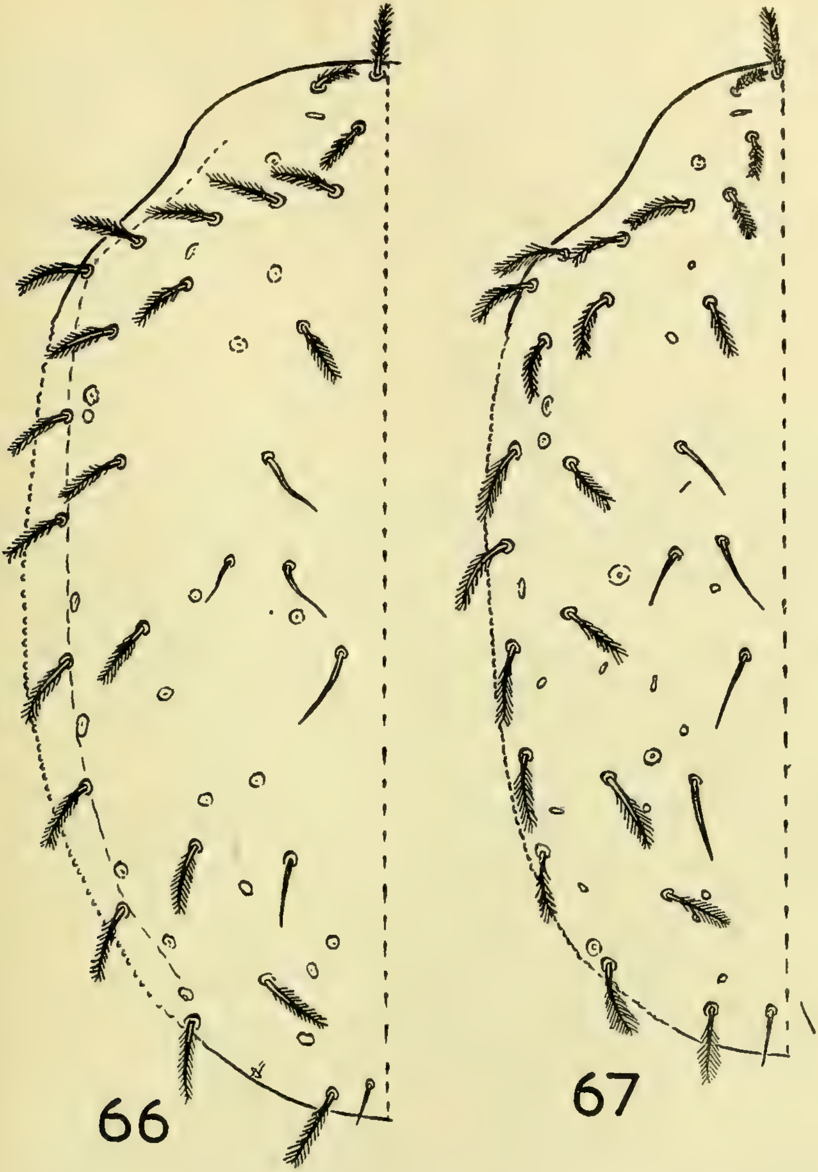
The key characters given above are based on the description and figures of this species by Valle (1953). The writers have not examined this species, which is recorded by Halbert (1915) from a number of localities in Ireland and by Hull (1918) from Ninebanks, Northumberland.

Geholaspis (Longicheles) mandibularis (Berl.)

Holostaspis mandibularis Berlese, A. (1904). *Redia*, **1** : 263.
? *Macrocheles minimus* Hull, J. E. (1918). *Trans. Nat. Hist. Soc. Northumb.* N.S. **5** : *73, fig.*
Geholaspis (*Longicheles*) *mandibularis*, Valle, A. (1953). *Redia* **38** : 344, figs.

FEMALE The dorsal shield is densely covered with minute tubercles and bears twenty-eight pairs of setae, of which twenty-two pairs are strongly plumose. The distribution of setae in the posterior half of the shield shows some variation in the material examined. The normal chaetotactic pattern is shown in Text-fig. 66 and a variant in Text-fig. 67. The lateral margins of the shield are conspicuously serrated. The vertical setae lie in close proximity to each other ; setae M1 are strongly plumose. The extra-marginal setae are plumose and increase in length towards the posterior end of the idiosoma.

The lacinae of the tritosternum are long and pilose. The sternal shield is ornamented with strong ridges and tubercles ; the three pairs of sternal setae are simple. The elongate metasternals each carry a simple seta. The genital shield is ornamented with punctate lines ; the genital setae are simple. The ventri-anal shield is evenly reticulated and tuberculated, and is provided with five pairs of pre-anal setae of which the external posteriors are pilose. The shape of the shield and the length of the setae show considerable variation in the specimens examined (cf. Text-figs.



FIGS. 66–67. Variation in the chaetotaxy of the dorsal shield of *Geholaspis* (*Longicheles*) *mandibularis* (Berl.), female.

68–70). The metapodals are elongate and weakly sclerotized. The posterior half of the peritrematal shield is free.

The external posterior rostrals lie well in advance of the internals and the ventral groove is provided with five transverse rows of denticles. The corniculi are long and slender and extend beyond the middle of the palp femur. The form of the tectum is shown in Text-fig. 71. The chelicerae are very long and strongly toothed (Text-fig. 72).

Leg I (approx. 600μ in length) with the tibia (approx. 100μ.) shorter than the tarsus (approx. 130μ).

DIMENSIONS. Female: length, 750–800μ; breadth, 480–500μ.

HABITAT AND LOCALITY. In litter, moss and compost. Widely distributed in Europe (Franz, 1954).

Genus ***MACRHOLASPIS*** Oudemans.

Macrholaspis Oudemans, A. C. (1931). *Ent. Ber.* 8, No. 180 : 272.

This genus was proposed by Oudemans (1931) for *Gamasus opacus* C. L. Koch and was characterized by the female having only two pairs of setae on the ventri-anal shield (" Ventrianaalschild mit 2 paar borstels "). According to Oudemans one of these two pairs of setae would be the para-anals and the other the pre-anals. Recently, the writers have examined a preparation and an unpublished drawing of *opacus* from the Oudemans Collection at Leiden, and found that the ventri-anal shield of the female, the only sex known, has two pairs of pre-anal setae and not one pair as Oudemans has stated. Further, *Nothrholaspis aciculatus* Berl., a common European species, was found to be synonymous with *Macrholaspis opacus* (Koch) Oudemans, 1931.

The following is an emended definition of the genus *Macrholaspis* :

Dorsal shield strongly attenuated posteriorly and bearing twenty-nine pairs[1] of plumose setae. Lateral margins of the shield markedly serrated. Sternal shield with three pairs of setae ; metasternals free. Genital shield with accessory sclerites and a pair of genital setae. Ventri-anal shield with *two* pairs of pre-anal setae. Other characters as in *Macrocheles*.

TYPE. *Gamasus opacus* C. L. Koch, 1839.

Two species are represented in the British fauna, these may be separated as follows :

1. Dorsal shield with 58 setae ; M1 short and straight (Text-fig. 73). Serrations of the lateral margin of the shield small and rounded (Text-fig. 74). Sternal shield with numerous punctures. Posterior margin of trochanter IV smooth *Macrholaspis opacus* (C. L. Koch)

–. Dorsal shield with 59 setae ; M1 long and curved distally (Text-fig. 78). Serrations of the lateral margin of the shield considerably longer and tapering (Text-fig. 80). Sternal shield with a network of ridges and punctures. Trochanter IV with a strong tubercle on its posterior margin . . . . . . *Macrholaspis dentatus* sp. n.

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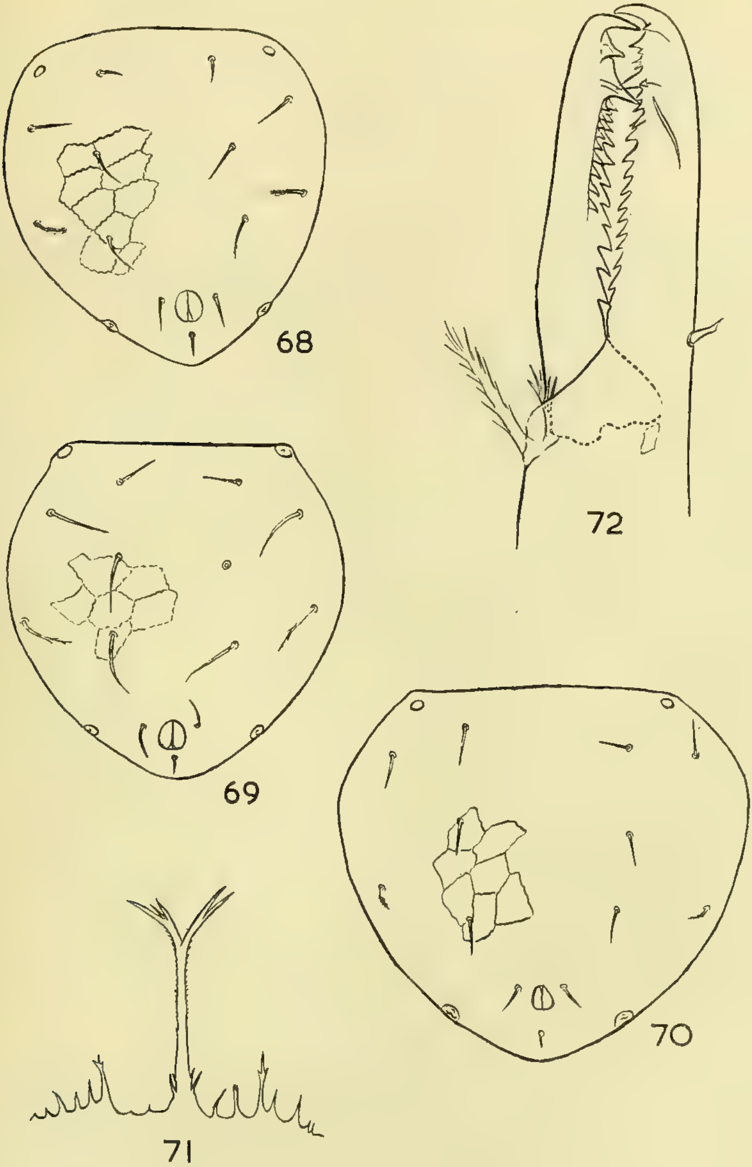
[1] An additional seta may be present in some species (cf. *Macrholaspis dentatus* sp. n.).



FIGS. 68–72. *Geholaspis* (*Longicheles*) *mandibularis* (Berl.), female. Figs. 68–70, variation in the form of the ventri-anal shield. Fig. 71, tectum. Fig. 72, chelicera.

Macrholaspis opacus (C. L. Koch)

Gamasus opacus Koch, C. L. (1839). *Deutsch. Crust. Myr. Arach.* fasc. 25, t. 24.
Macrocheles (*Nothrholaspis*) *aciculatus* Berlese, A. (1918). *Redia* **13** : 169 syn. nov.
Holostaspis terreus, Halbert, J. N. (1915). *Proc. Roy. Irish Acad.* **31**, ii : 66.
Macrholaspis opacus, Oudemans, A. C. (1931). *Ent. Ber.* **8**, No. 180 : 272.
Nothrholaspis aciculatus, Willmann, C. (1939). *Ark. Zool.* **31** A, 10 : 6, figs.
Macrocheles (*Nothrholaspis*) *terreus*, Cooreman, J. *Bull. Mus. roy. Hist. nat. Belg.* **19**, 63 : 21.

Female. Dorsal shield strongly attenuated posteriorly (Text-fig. 13) and characteristically ornamented in its anterior third with a polygonal network of minute spines (*aciculatus* !). The lateral margins of the shield are distinctly serrated (Text-fig. 74). The vertical setae are strongly developed ; setae M1 are short and plumose (Text-fig. 75). The remaining twenty-seven pairs of plumose setae are distributed as in Text-fig. 73. The extra-marginal setae are of the same form as the marginal series.

The tritosternum is normal with the lacinae pilose. The sternal shield is densely covered with punctures and bears three pairs of simple setae (Pl. 4, fig. 18). The metasternal setae are also simple. The genital shield is covered with punctures which tend to form a network in its anterior two-thirds. Accessory sclerites are well developed and the genital setae are plumose. The ventri-anal shield (approximately 220μ long and 198μ wide) is oval in outline and, like the dorsal shield, ornamented with spinules. The two pairs of pre-anal setae are plumose, the para-anals long and simple, and the post-anal seta strongly plumose. The interscutal membrane between the genital and ventri-anal is provided with three pairs of platelets, one pair of pore-bearing platelets and a pair of plumose setae. The metapodal shields are conspicuous. The peritreme and peritrematal shield are normal.

The gnathosoma bears four pairs of setae ventrally. The ventral groove has five transverse rows of denticles. The form of the tectum is shown in Text-fig. 76. Both digits of the chelicera are bi-dentate ; the distal tooth on the fixed digit is small and difficult to see if the chelicera is not orientated correctly (Text-fig. 77). The *pilus dentilis* is long and stout. The dorsal seta is comb-like.

Leg I (530μ) has plumose setae on the femur, genu and tibia. Tibia I (85μ) is considerably shorter than the tarsus (121μ). Legs II to IV measure 550μ, 495μ and 800μ, respectively.

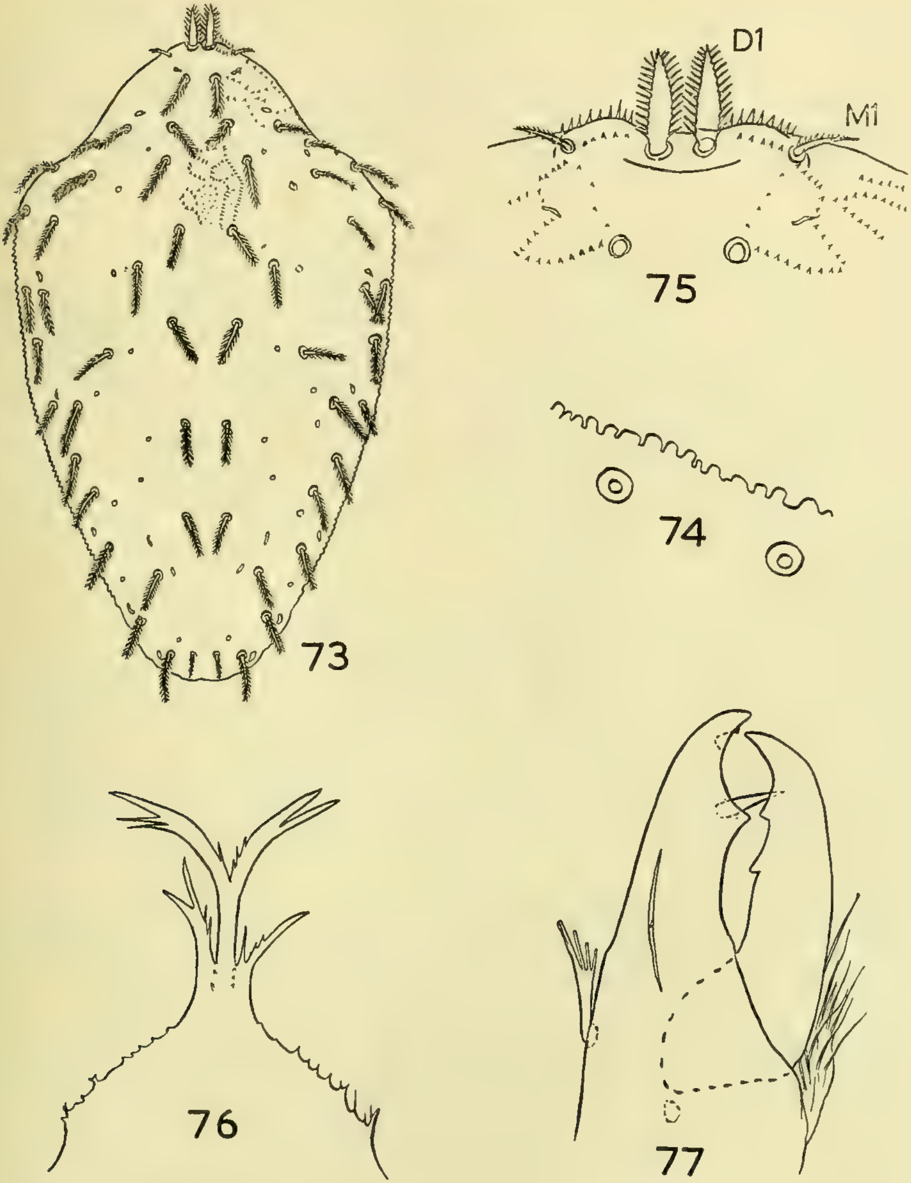
Male. Unknown.

Dimensions. Female ; length 725–740μ ; breadth 445–470μ.

Habitat and locality. Widely distributed in Europe. Common is decaying wood, moss and litter.

Macrholaspis dentatus sp. n.

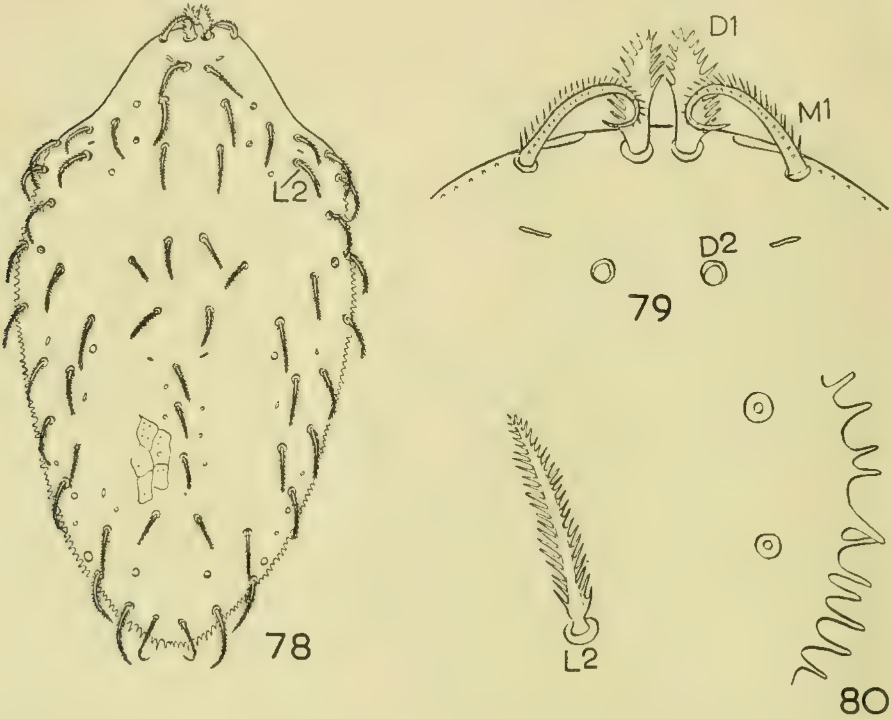
Female. Dorsal shield attenuated posteriorly as in the preceeding species but without spinules. The ornamentation consists of a network of lines and punctures (Text-fig. 78). The chaetotaxy of the shield comprises fifty-nine setae arranged as in the figure. The verticals are stout and setae M1 long, plumose and curved (Text-fig. 79). An interesting feature of the chaetotactic pattern is the presence of three



Figs. 73–77. *Macrholaspis opacus* (C. L. Koch), female. Fig. 73, dorsal shield. Fig. 74, lateral margin of dorsal shield. Fig. 75, anterior region of dorsal shield. Fig. 76, tectum. Fig. 77, chelicera.

unpaired setae in the dorsal series. The lateral margins of the shield are strongly serrated (Text-fig. 80). The extra-marginal setae are similar to the marginals.

The sternal shield is provided with a network of ridges and punctures and bears three pairs of simple setae (Pl. 4, fig. 19). The metasternal shields are small and free, and the setae simple. The genital shield is strongly ornamented with a network of ridges and punctures ; the genital setae are plumose. The ventri-anal shield, similarly ornamented, measures 187μ in length and 145μ in breadth, and bears two pairs of plumose pre-anal setae. The para-anals are long and simple, and the post-anal seta short and plumose. The interscutal membrane between the genital and ventri-anal shields is provided with platelets and plumose setae as in the preceding species. The peritreme and peritrematal shield are normal.



Figs. 78–80. *Macrholaspis dentatus* sp. nov., female. Fig. 78, dorsal shield. Fig. 79, anterior region of dorsal shield. Fig. 80, lateral margin of dorsal shield.

The chaetotaxy and structure of the gnathosoma are essentially the same as in *opacus*. The form of the tectum and the dentition of the chelicerae are also similar.

Leg I, approximately 525μ in length, has the tibia considerably shorter than the tarsus (tibia, 88μ; tarsus, 110μ). Legs II to IV measure 575μ, 560μ and 880μ in length, respectively.

Dimensions. Length 765μ; breadth 430μ.

Habitat and locality. A single female from humus under bracken in the Leri Valley, North Cardiganshire, Wales. Holotype female, 1955.10.22.95.

This species is characterized by the form of setae M1, the ornamentation of the sternal shield and the shape of the ventri-anal shield.

Genus *HOLOSTASPELLA* Berl.

Holostaspella Berlese A. (1904). Redia **1** : 241

Dorsal shield with twenty-eight pairs of setae. Vertical setae situated on an outgrowth of the dorsal shield. Sternal shield with three pairs of setae; metasternal shields free. Ventri-anal shield with four pairs of pre-anal setae. Gnathosoma normal. Leg I in the female armed with stout spurs. Other characters as in *Macrocheles* Latr.

Type. *Holostaspis* (*Holostaspella*) *sculpta* Berl., 1904.

This genus is represented in Britain by one species only.

Holostaspella ornata (Berl.)

Macrocheles vagabundus, Oudemans, A. C. (1902). *Tijdschr. Ent.* **45** : 43, figs.
Holostaspis ornatus Berlese, A. (1904). *Redia* **1** : 277.
Holostaspella ornata Oudemans, A. C. (1931). *Ent. Ber.* **8** : 273, syn. nov.
Holostaspella ornata, Evans, G. O. (1956). *Proc. Linn. Soc. Lond.*

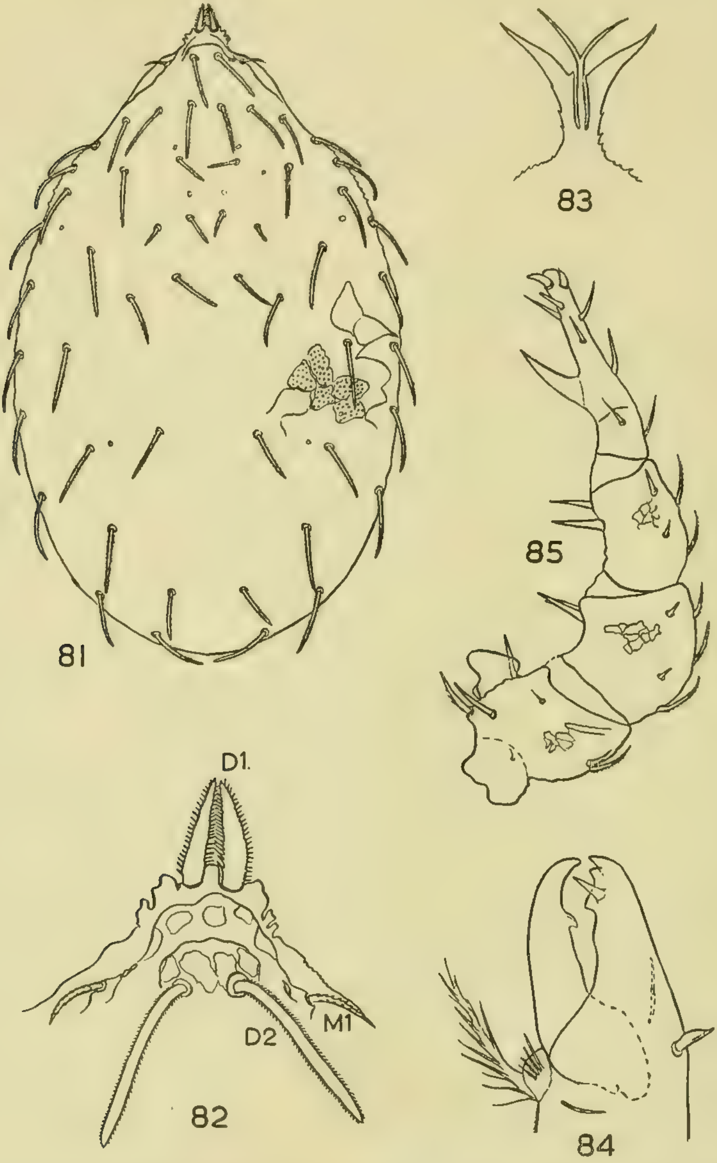
Female. Dorsal shield, finely reticulated, bears twenty-eight pairs of setae (Text-fig. 81). The verticals are stout and pilose, and are situated on a prominent projection (Text-fig. 82). The setae on the shield are minutely pilose as shown in the figure.

The sternal shield is massive and characteristically ornamented with ridges and depressions (Pl. 4, fig. 20). The first pair of sternal setae are strongly plumose; the second and third pair smooth. The metasternals, triangular in outline, each bear a simple seta. The large genital shield is richly ornamented; the genital setae simple. Most of the region posterior to coxae IV is occupied by the heavily ornamented ventri-anal shield (335 × 315μ), which bears four pairs of pre-anal setae in addition to the para-anals and the post-anal seta. The anterior pre-anal is weakly pilose and the post-anal plumose. The interscutal membrane is coarsely striated.

The gnathosoma is normal for the *Macrochelinae*. The lateral processes of the tectum are free (Text-fig. 83). The dentition of the chelicera is shown in Text-fig. 84.

Leg I with the tibia (121μ) shorter than the tarsus (132μ). The femur and trochanter of leg II are spurred; the tarsus has a large stout spine ventrally (Text-fig. 85).

Male. Unknown.



FIGS. 81–85. *Holostaspella ornata* (Berl.), female. Fig. 81, dorsal shield. Fig. 82, anterior region of dorsal shield. Fig. 83, tectum. Fig. 84, chelicera. Fig. 85, leg II (ambulacrum omitted).

DIMENSIONS. Length 924–950μ; breadth 550–560μ.

HABITAT AND LOCALITY. This species has previously been recorded from the Netherlands (Oudemans, 1902) and Austria (Franz, 1954). The writers have examined a single specimen taken from *Sphaerocerus* sp. captured at Bagley Wood, Berks (Coll. O. W. Richards, det. Vitzthum). The above description and figures are based on the type from the Oudemans Collection, Leiden.

SUMMARY

1. The classification of the *Macrochelidae* is discussed and keys are given for the identification of British species of the *Macrochelinae*.

2. The following three new species are described and figured:

Macrocheles rothamstedensis sp. nov.
Macrocheles punctoscutatus sp. nov.
Macrholaspis dentatus sp. nov.

3. The following species are recorded for the first time from Britain:

Macrocheles carinatus (C. L. Koch)
Macrocheles decoloratus (C. L. Koch)
Macrocheles insignitus (Berl.)
Macrocheles montanus (Willmann)
Macrocheles penicilliger (Berl.)
Macrocheles subbadius (Berl.)
Macrocheles tardus (C. L. Koch).
Geholaspis (*Longicheles*) *mandibularis* (Berl.)
Holostaspella ornata (Berl.)

4. The following species have been relegated to the synonymy:

Nothrholaspis aciculatus Berl., 1918 syn. of *Macrholaspis opacus* (C. L. Koch) 1839.
Holostaspella ornata Oudemans, 1931, syn. of *Holostaspella ornata* (Berl.), 1904.
Macrocheles gladiator Hull, 1918, syn. (?) of *Macrocheles plumiventris* Hull, 1918.
Macrocheles plumipes Hull, 1918, syn. (?) of *Macrocheles plumiventris* Hull, 1918.
Macrocheles minimus Hull, 1918, syn. of *G.* (*Longicheles*) *mandibularis* (Berl.), 1904.
Macrocheles hulli Falconer, 1923, syn. of *Macrocheles carinatus* (C. L. Koch), 1839.
Macrocheles occidentalis Hull, 1925, syn. of *Macrocheles submotus* Falconer, 1924.
Macrocheles gloriosus Hull, 1925, syn. of *Macrocheles submotus* Falconer, 1924.
Nothrholaspis fimicola Sellnick, 1932, syn. of *Macrocheles plumiventris* Hull, 1925.
Coprholaspis anglicus Turk, 1946, syn. of *Macrocheles glaber* (Müller), 1860.

ACKNOWLEDGMENTS

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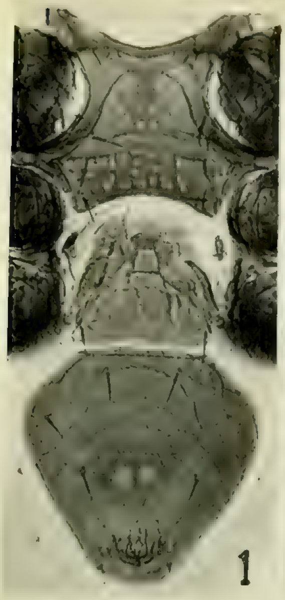
EXPLANATION OF PLATES

PLATE I

Sternal, genital and ventri-anal shields of the females of :

FIG. 1. *Macrocheles muscaedomesticae* (Scopoli). × 95.
FIG. 2. *Macrocheles rothamstedensis* sp. nov. × 153.
FIG. 3. *Macrocheles glaber* (Müller). × 115.
FIG. 4. *Macrocheles punctoscutatus* sp. nov. × 110.
FIG. 5. *Macrocheles subbadius* (Berl.). × 160.
FIG. 6. *Macrocheles insignitus* Berl. × 218.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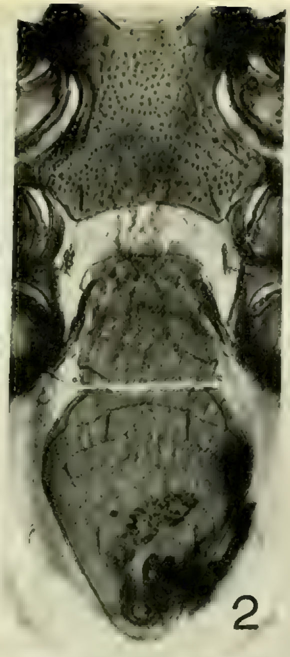
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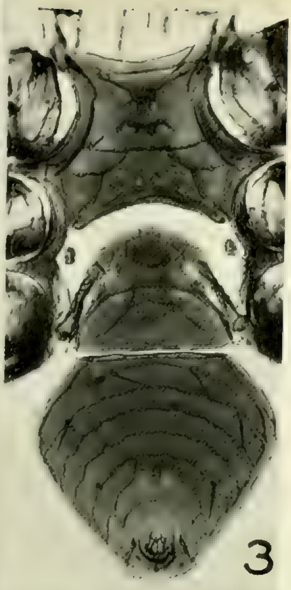
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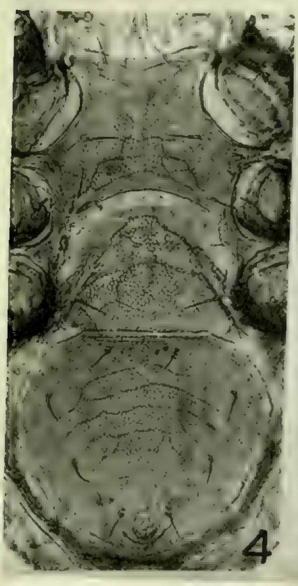
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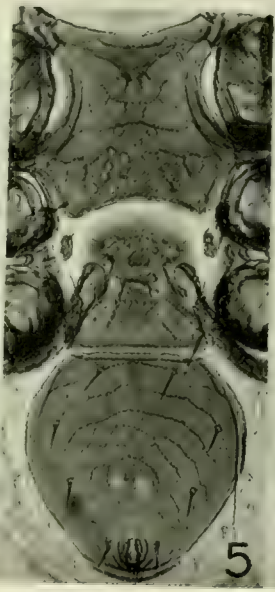
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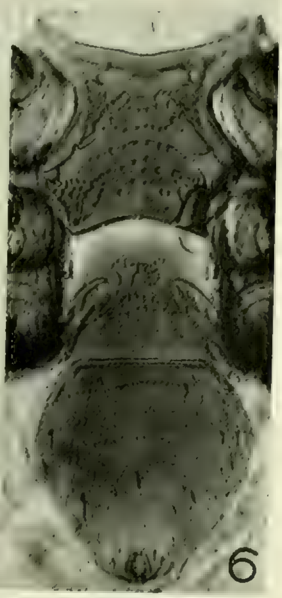
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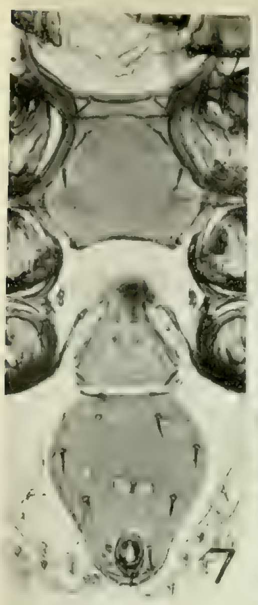
PLATE 2

Sternal, genital and ventri-anal shields of the females of :

FIG. 7. *Macrocheles merdarius* (Berl.). × 199.
FIG. 8. *Macrocheles montanus* (Willmann). × 100.
FIG. 9. *Macrocheles carinatus* (C. L. Koch). × 100.
FIG. 10. *Macrocheles penicilliger* (Berl.). × 110.
FIG. 11. *Macrocheles submotus* Falconer. × 90.
FIG. 12. *Macrocheles tardus* (C. L. Koch). × 110.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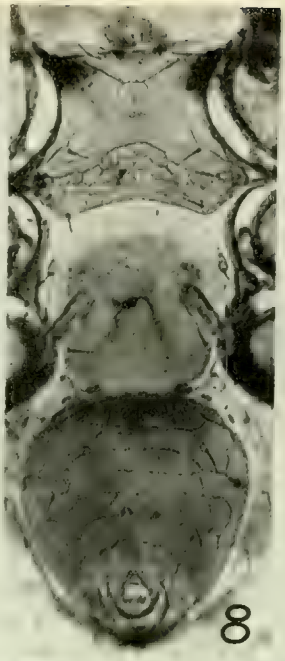
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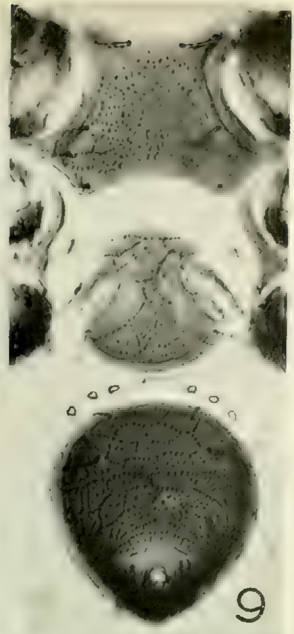
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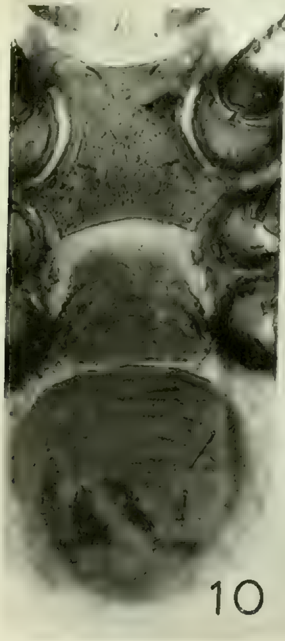
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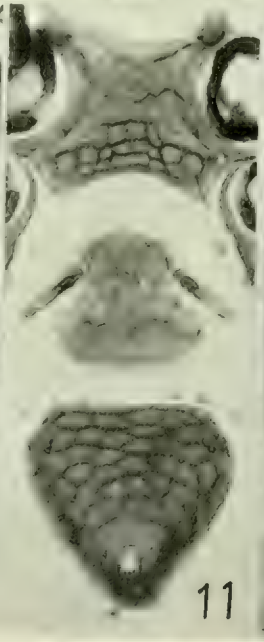
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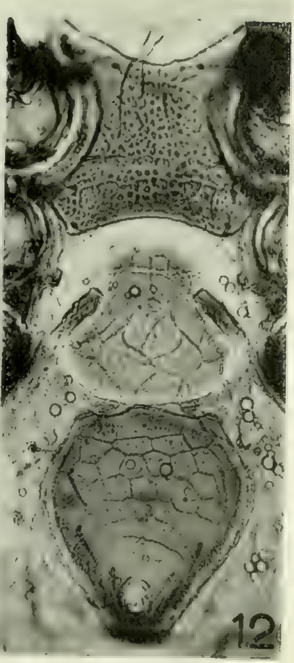
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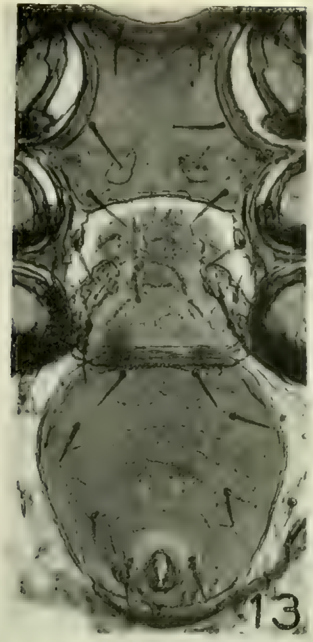
PLATE 3

Sternal, genital and ventri-anal shields of the females of :

FIG. 13. *Macrocheles decoloratus* (C. L. Koch). × 120.
FIG. 14. *Macrocheles matrius* Hull. × 112.
FIG. 15. *Macrocheles plumiventris* Hull. × 74.
FIG. 16. *Macrocheles superbus* Hull. × 70.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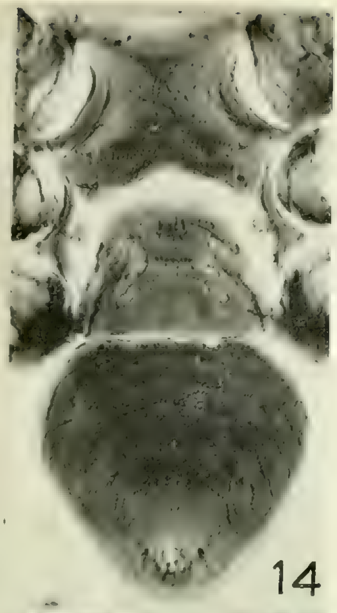
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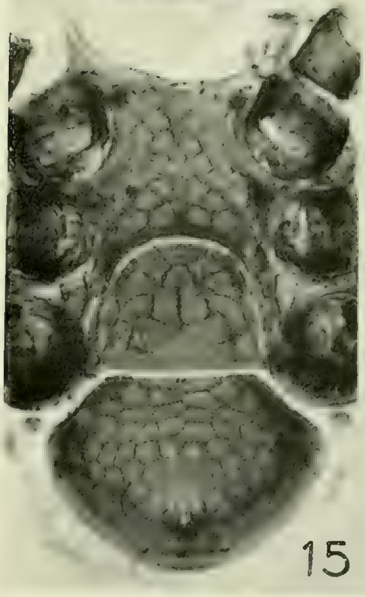
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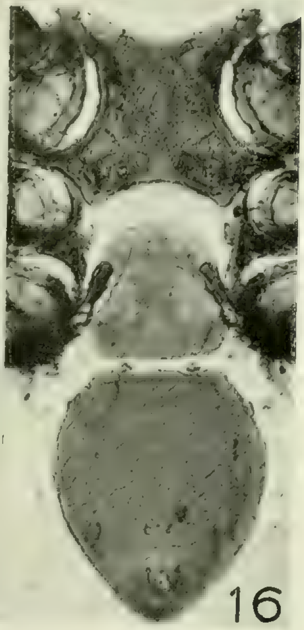
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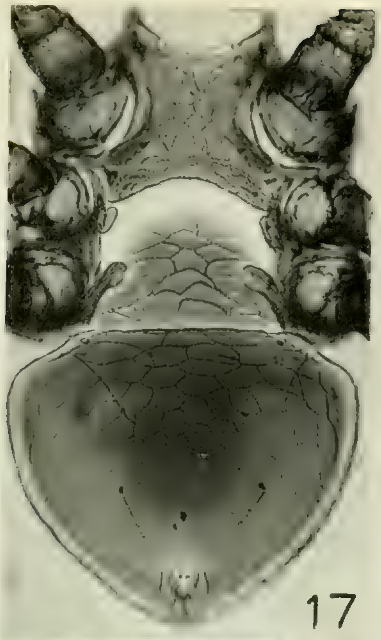
PLATE 4

Sternal, genital and ventri-anal shields of the females of:

FIG. 17. *Geholaspis (Geholaspis) longispinosus* (Kramer). × 100.
FIG. 18. *Macrholaspis opacus* (C. L. Koch). × 153.
FIG. 19. *Macrholaspis dentatus* sp. nov. × 131.
FIG. 20. *Holostaspella ornata* (Berl.). × 123.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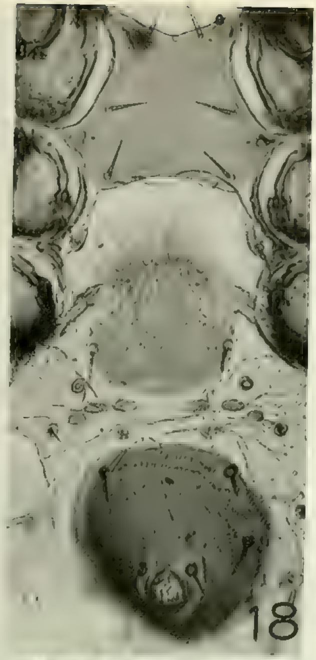
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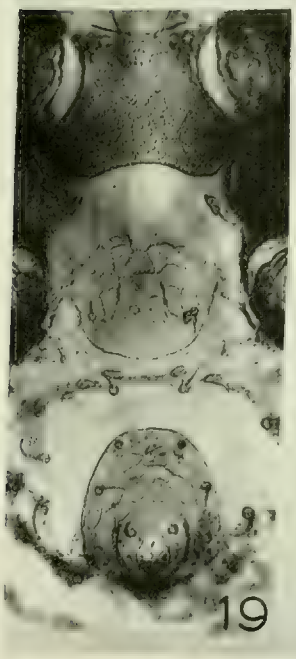
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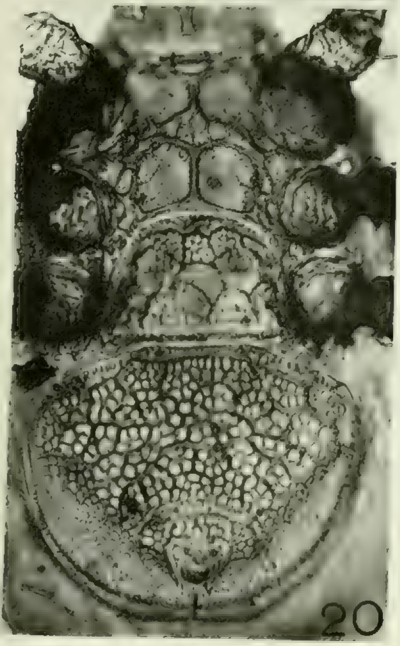
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THE EVOLUTION OF RATITES

PRESENTED

SIR GAVIN de BEER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
ZOOLOGY Vol. 4 No. 2
LONDON: 1956

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BY

SIR GAVIN de BEER, F.R.S.

Pp. 57–70 ; *Plates* 5–9

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THE EVOLUTION OF RATITES

By Sir GAVIN de BEER, F.R.S.
Director, British Museum (Natural History).

SYNOPSIS

Adequate knowledge of the structure of *Archaeopteryx* now enables a comparison to be made between it and the Carinates. In the latter the structure of the wing, the tail, and the cerebellum can be shown to be adaptations to flight. Since these same adaptations are found in Ratites, they would be inexplicable unless the Ratites were descended from flying birds. The palate of the Ratites is not primitive but neotenous, and represents an early stage through which the palate of many Carinates passes during development. Other neotenous features of the Ratites are the plumage and the persistence of sutures between the bones of the skull.

INTRODUCTION

In the first edition of the *Origin of Species* (1859, p. 134) Darwin wrote: " As Professor Owen has remarked, there is no greater anomaly of nature than a bird that cannot fly; yet there are several in this state." There was a touch of irony in making this quotation, for as is well known, Owen's views on evolution were uncertain and equivocal, and the very existence of flightless birds was inescapable evidence of descent with modification from the " archetype " of birds. Darwin himself continued: " We may believe that the progenitor of the ostrich genus had habits like those of the bustard, and that, as the size and weight of its body were increased during successive generations, its legs were used more, and its wings less, until they became incapable of flight."

A few years later, in his treatise on *The Anatomy of Vertebrates* (1866, **2**, 12.) Owen put forward the view that the Cursores or Ratites were not " a natural order; some of its exponents have demonstrably closer affinities to other groups of which they are wingless members." Further on (*loc. cit.*: 43), Owen referred to the Ratites as " those birds in which the power of flight is abrogated ". For a man who did not believe unreservedly in evolution, this was about as near as he could get to the view that the Ratites are descended from flying birds, and he even supplied the explanation of such a descent (*loc. cit.*: 12): " by the arrested development of the wings unfitting them for flight ".

The view of the degenerate nature of the Ratites has been supported by M. Fürbringer (1888), T. J. Parker (1892), W. P. Pycraft (1901), R. Broom (1906), J. E. Duerden (1920), E. Stresemann (1927–34), W. K. Gregory (1935), and many others; and it might have been thought that the evolution of flightless birds from flying birds was generally accepted. Nevertheless the hypothesis has been put forward that the structure of the Ratites is in many respects so primitive that they must have branched off from the main stem of bird evolution before the power of flight was acquired. B. Lindsay (1885), R. S. Wray (1887), A. C. Chandler (1916) and J. C. Ewart (1921) are of this opinion, but the foremost exponent of this view has been P. R. Lowe (1928, 1935), with whom M. Friant (1945, 1946) has expressed agreement.

It has been known for a long time that the Ratites show a number of characters which have been considered as primitive. Among these is the palate, on which T. H. Huxley (1867) based a system of classification of the birds in which the dromaeognathous type, characteristic of the Ratites, was regarded as the most primitive. Pycraft (1900, 1901) who extended Huxley's observations, summed up (1901 : 343) the situation as he saw it in the words : " The contention that the Struthious (Palaeognathine) palate is of a more ancient type than the Neognathine is admitted by all." The term palaeognathine or palaeognathous is equivalent to dromaeognathous, while neognathine or neognathous includes all the other categories of Huxley's classification.

This argument has been adopted by Lowe, in whose view the Ratites show " the primitive palate from which the neognathous palate characteristic of the modern or flying birds was obviously derived ". To this Lowe has added six further arguments, all in support of his view that the ancestors of Ratites never flew. They are :

1. The " primitive " disposition of the muscles.
2. The fact that " *all* the feathers borne by the adult ostrich or by any other struthious form whether they are situated on the wing, or body generally, are nothing more than down, or modified down," and being juvenile structures are he thinks therefore ancestral and primitive.
3. The absence of the rudiment of the clavicle in the embryo of the ostrich, which, in his view, is proof that the ostrich decended from ancestors which had lost the clavicle, and therefore not from flying birds in which the clavicle is preserved.
4. The persistence of the sutures in the skull of the ostrich, in which it resembles the condition of the ancestral reptiles and differs from that of flying birds in which the bones of the skull are firmly fused in the adult.
5. The obtuse angle subtended between the coracoid and the scapula, which resembles the condition of the ancestral reptiles and differs from that of flying birds where this angle is more or less acute.
6. The similarity between the bones of the hand of the ostrich and those of a dinosaur such as *Ornitholestes*.

With perfect logic, Lowe contended that if, as he believed, the Ratites were descended from birds which had never acquired the power of flight, then it must follow that *Archaeopteryx* could not have been in the line of ancestry of birds, but must have been an independent offshoot from the reptiles.

The detailed knowledge now available of the structure of *Archaeopteryx* (de Beer, 1954*b*) can be used to test this hypothesis. Two related problems are involved : the evolution from reptiles of birds in general, and the evolution of Ratites in particular. These problems can be solved by finding the answers to the following three questions :

1. Is *Archaeopteryx* on the line of evolution from reptiles to birds?
2. Are there any characters by which modern flying birds differ from *Archaeopteryx* which can be attributed with certainty to adaption to active flight?
3. Are these characters also shown by the Ratites?

ARCHAEOPTERYX AND THE ANCESTRY OF BIRDS

If *Archaeopteryx* was the product of an independent line of evolution from the reptiles, unrelated to the stock which gave rise to birds, it then becomes necessary to believe that the feathers of *Archaeopteryx* and the feathers of all other birds were independently evolved. The identical details of structure which the feathers show involve the quill, the vane formed of barbs, held together and parallel with one another and yet capable of being torn apart, the proportions between the vane and the quill and between the proximal and distal portions of the vane. In all these respects, the structure of the feather in *Archaeopteryx* and in modern flying birds is so exactly identical that it is impossible to believe that they were independently evolved.

But this is not all. In addition to the feathers themselves, there is the manner in which they are arranged on the wing, the differentiation between larger feathers or remiges and smaller feathers or coverts, and the further differentiation of the remiges into primaries, borne on the wrist-joint and hand, and secondaries borne on the forearm. Here again the conditions are identical in *Archaeopteryx* and in modern flying birds. It follows that the view that *Archaeopteryx* is not related to the modern birds is completely untenable.

Granting that *Archaeopteryx* represents an example of an early stage in the evolution of feathered organisms away from the reptiles, it may still be asked whether *Archaeopteryx* is ancestral to modern birds. The remarkable mosaic of reptilian and avian characters that *Archaeopteryx* shows has been discussed elsewhere (de Beer, 1954*a*). The conclusion to be drawn is that *Archaeopteryx* is a *rara avis* among fossils in that it is possible to say that nothing is known, either by way of structures which it possesses or does not possess, or of the time-relations of its occurrence, which might disqualify it from being regarded as a true ancestor of modern birds. As G. G. Simpson (1936 : 92) has said, " every difference between *Archaeopteryx* . . . on one side and true reptiles of possible ancestral type, especially the Pseudosuchia, on the other, is definitely in the direction of true birds ".

If, as H. Steiner (1918, 1956) believes, *Archaeopteryx* was aquintocubital, it would provide yet another proof that it was ancestral to modern birds.

CARINATES AND ADAPTATIONS TO FLIGHT

Accepting the fact that *Archaeopteryx* is a mile-stone on the road from reptiles to modern birds and represents the type of structure from which Carinates evolved, attention may be turned to the question whether any of the differences observable between *Archaeopteryx* and the modern flying birds or Carinates can with certainty be ascribed to adaptation to flight. That the flying bird is highly adapted to its mode of life is a commonplace of biological expression, and in the case of some structures it is easy to prove it. Attention will here be confined to the carpometacarpus, the pygostyle, and the cerebellum. The keel on the sternum is deliberately omitted from the discussion since its absence in the Ratites is the basis of their diagnosis, and the question at issue is whether this absence is primitive or specialized.

The carpometacarpus is the product of fusion between the distal carpals and the three metacarpals, the 2nd and 3rd of which are fused again at their distal extremities. The result is a structure providing a light and resilient yet firm basis for the attachment of the primary remiges. It is absolutely characteristic of modern birds and found nowhere else.

In *Archaeopteryx* the forelimb skeleton consists of proximal carpals, the radiale and ulnare which remain more or less separate, distal carpals fused together and to the base of the third metacarpal, and separate and independent 1st and 2nd metacarpals. *Archaeopteryx* was unable to do much more than glide, and as Dr. H. W. Parker has remarked to me, the air-pressure on the feathers of its wings must have been lower than in an actively flying bird with the same ratio of wing-area to mass, because *Archaeopteryx* was unable to maintain itself in the air continuously against the pull of gravity. The carpometacarpus of the Carinate is without doubt an adaptation to flight by enabling the wing to exert and withstand greater pressure.

There is one further feature of the wing of Carinates that calls for notice, and that is the presence of a small number of feathers attached to the first digit of the hand, forming a " bastard wing ". These few feathers add nothing to the weight-bearing power of the wing, yet they perform a function of capital importance in flight for they serve like the slotted wing of a modern aircraft to maintain a slip-stream of air and prevent stalling. The " bastard wing " is a beautiful adaptation to flight.

In *Archaeopteryx* the tail is very long, as long as the rest of the body, and its skeleton consists of 20 elongated separate vertebrae, to each of the hinder 15 of which correspond a pair of rectrices, quill-feathers, which form an oblong and elongated air-resisting surface. In Carinates the tail is very short, consisting of about a dozen flattened vertebrae, the hindmost half-dozen or so of which are fused together, giving rise to a pygostyle. The rectrices, to the number of a dozen pairs, are disposed transversely. A masterly analysis and comparison of the conditions in the tail of *Archaeopteryx* and Carinates has been given by H. Steiner (1938).

It has been pointed out by J. Maynard Smith (1952) that the structure of the most primitive flying animals is one that imparts aerodynamic stability. That is to say that they are of a shape such that when in " flight " through the air, they are able to maintain the direction of their progress without muscular intervention and compensatory movements. In other words, such animals are gliders, and the structure of the skeleton, wings, and tail of *Archaeopteryx* is just such as would have enabled it to glide with stability, but not fly actively. The perfection of the power to fly has involved the development of the ability to perform mechanically unstable flight-movements, such as rapid pitching, yawing, and banking, for which a reduction of the long axis of the animal is essential. The pygostyle of the Carinates is without doubt an adaptation to flight.

The cerebellum of *Archaeopteryx* is best characterized negatively by saying that it is small and does not overlap forwards over the midbrain. In other words, the brain of *Archaeopteryx* is similar to that of reptiles. In Carinates, on the other hand, the cerebellum is so large that it expands forwards as a median and unpaired structure over the dorsal surface of the midbrain, which it presses downwards, and so the cerebellum comes into contact with the hinder part of the cerebral hemisphere. The result is that the cerebellum of Carinates hides the optic lobes, whereas the latter structures are plainly visible in *Archaeopteryx*.

The cerebellum has been defined by Sherrington as the head-ganglion of the proprioceptive system. As L. Edinger (1912 : 300) has shown in *Columba*, among the most important sources of impulses conducted to the cerebellum are the organs of balance in the semi-circular canals of the ear, which respond not only to changes in static conditions, but also to changes in the dynamic conditions of the organism caused by alterations in speed and direction of motion. In the case of Carinates, as flying birds the possibilities of direction of motion are greatly increased by the introduction of the vertical dimension. At the same time, the performance of flight requires high speed of adjustment and compensatory movements, not only in actual flight but in landing on small objects. As J. Z. Young (1950 : 455) has said, there is reason to think that the large size of the cerebellum in flying birds is connected with the precise control of movement in all planes of space during flight.

The view that the cerebellum of Carinates is an adaptation to flight is confirmed by the conditions in the pterosaurs. There, as T. Edinger (1941 : 678) has shown, there is " a cerebellum thrust forward above the midbrain to adjoin the forebrain as in birds ; obviously this is one of the characters distinguishing all pterosauria from the other reptiles ". There can be no doubt that the parallel development and large size of the cerebellum in pterosaurs and in birds, by which they both differ from all non-pterosaurian reptiles, are due to the same cause : adaptation to flight.

Having now established that the carpometacarpus, the " bastard wing ", the pygostyle, and the large size of the cerebellum of Carinates are adaptations to flight, attention may be turned to the conditions in Ratites in respect of these structures.

ADAPTATIONS TO FLIGHT IN RATITES

The skeleton of the wing of Ratites is built on identically the same plan as that of the Carinates. B. W. Tucker (1938*a* : 224) has stressed the similarity not only in the points of fusion between the various elements which go to make up the carpometacarpus in both Carinates and Ratites, but also subtle points, such as the curvatures of the 2nd and 3rd metacarpals and the expansion of the basal phalanx of the 3rd digit.

H. Steiner (1949 : 367) has studied the wings of Carinates and Ratites by means of X-rays and concludes that it " lässt sich ohne jeden Zweifel feststellen, dass genau die gleichen Eigentümlichkeiten zu beachten sind. Ausgehend von irgend einem Carinatenflügel kann ausserdem über den Flügel von *Rhea* und *Struthio* bis zu jenem von *Casuarius* eine zunehmende Verkümmerung verfolgt werden, welche über die Zustände, wie sie bei *Dromaeus* und *Apteryx* angetroffen werden, bis zur vollständigen

Reduktion des Flügels bei den ausgestorbenen Riesenstraussen *Aepyornis* und *Dinornis* geführt hat ".

There can be no doubt that the skeleton of the wing in the Ratites shows features associated with adaptation to flight which are explicable only on the view that they were inherited from ancestors which flew.

The skeleton of the tail in Ratites has been studied by W. Marshall (1873) and referred to by W. K. Gregory (1935), but otherwise has not attracted much attention. It is composed of a varying small number of vertebrae which in some forms decrease in size caudally and taper out. But in the ostrich there is a structure composed of the fusion of the terminal vertebrae which undoubtedly constitutes a pygostyle. It is shown in Pl. 5 in comparison with a Carinate pygostyle. Since this structure in Carinates is certainly associated with the power of flight, its presence in a Ratite is inexplicable unless the ancestors of Ratites also flew. This has also been pointed out by Gregory.

The cerebellum of birds has been subject to an exhaustive study by S. Ingvar (1918), the results of which show that the large size of the cerebellum in Carinates is matched by a similar large size in Ratites. Not only does the cerebellum of the ostrich, for instance, project forwards over the dorsal surface of the mid-brain towards the cerebral hemisphere, but it shows the same *arbor vitae* structure as the cerebellum of a Carinate when seen in sagittal section. In Plate 6 are shown the brain of *Archaeopteryx* in side view, and sagittal sections through the brains of *Rhea* and *Tringa*. It is clear that the structure of the cerebellum is the same in the Ratites as in the Carinates ; and if its structure in the latter is an adaptation to flight, its structure in the former is inexplicable unless the Ratites were descended from flying birds.

On all three counts, the evidence is conclusive that the Ratites must have evolved from flying birds. It remains now to consider a few further points which receive ready explanation on this view, and to refute the grounds on which Lowe thought that the Ratites were primitively flightless.

It has been shown above that the skeleton of the wing of the Ratites bears evidence of adaptation to flight. It may be added that in one form, the *Rhea*, there is still to be seen a trace of the differentiation between primary and secondary remiges, as shown in Plate 7. This distinction, which already exists in *Archaeopteryx* would be meaningless unless the *Rhea's* ancestors had been capable of flight. Even more remarkable is the presence in the *Rhea* of feathers on the 1st digit forming a " bastard wing ", an adaptation evolved in Carinates which results in the maintenance of the slip-stream in flight.

The curious phenomenon of diastataxy or aquintocubitalism, the absence of the 5th secondary remex from the row of flight feathers in the wing, has long been a puzzle. Its most probable explanation has been provided by H. Steiner (1918) who has shown in a brilliant and exhaustive series of studies that it is associated with the peculiar method of folding the wing, the ulnar flexure, adopted by birds. When a bird folds its wings, the hand is moved sideways relatively to the forearm through an angle of almost 180°. The development of this new type of movement affected the feather-rudiments in the skin at the point of flexure and dislocated them in such a way that the rudiment which would have given rise to the 5th secondary remex is displaced, and, instead, develops into the 5th major covert, leaving a gap in the series of secondaries. Steiner has shown conclusively that in the Carinates the aquintocubital condition is primitive, and that the presence of the 5th secondary remex, which is found sporadically in some members of nearly all groups of birds, is due to a secondary readjustment. Be that as it may, it is clear that the phenomenon of aquintocubitalism is intimately associated with the structure and arrangement of the remiges in a flying wing. It is therefore remarkable that a vestige of the aquintocubital condition is found in the wing of the young *Apteryx* (Steiner 1918 : 434) which thereby is shown to possess a structure characteristic of primitive Carinates and which could not have been independently evolved. Professor Steiner has kindly informed me that he has evidence that other Ratites also are aquintocubital.

Further, there is another line of evidence relating to the loss of the power of flight of *Apteryx*. R. Broom (1947 : 49) has ingeniously shown that as New Zealand has had no land connexions with any other continent since early Jurassic times, and as the centre of evolution of birds exemplified by *Archaeopteryx* was situated in the Palaearctic continent in middle Jurassic times, the ancestors of *Apteryx* could not have reached New Zealand unless they flew thither.

THE NEOTENY OF RATITES

Reverting now to the reasons on which Lowe sought to base the view that the Ratites were primitive birds whose ancestors had never flown, one : the similarity between the hand of the ostrich and that of the dinosaur, has been dismissed as invalid. Tucker (1938*b*) has shown that such resemblances as there are between them are only superficial and without significance. Another : the angle between the coracoid and the scapula, can be shown to be due to the reduction of the length of the pectoral muscles in the Ratites ; for it is the lengthening of the coracoid in the Carinates which is responsible for the acuteness of the angle between the coracoid and the scapula; and the length of the coracoid may be regarded as an adaptation to flight since it is associated with the lengthening of the pectoral muscles.

Whether the disposition of the muscles in the Ratites is " primitive ", as Lowe has contended, is a matter for argument ; but what is no matter for argument is the explanation of the presence in the Ratites of nestling-down, permanent sutures between the bones of the skull, and the dromaeognathous structure of the palate. All these are demonstrably the result of neoteny or the secondary retention of features which were juvenile in the ancestors of the Ratites.

To begin with the feathers. It is well known that the down-feathers, nestling-down or neossoptyles, are nothing but the fluffed-out distal ends of the rudiments of the adult feathers or teleoptyles. In Carinates, particularly those in which the young are nidifugous and have a " chick " stage, the nestling-down is well developed, and it owes its fluffiness to the fact that the barbs have no hooks and therefore the feathers form no vanes. This nestling-down is subsequently discarded when the adult feathers or teleoptyles take the place of their former distal extremities the neossoptyles. That the Ratites are neotenous in retaining their " ostrich feathers " or nestling-down throughout life is admitted by Lowe himself (1935 : 420) : " So far as their feather covering is concerned the Struthiones are big, overgrown chicks. They are the " Peter Pans " of the avian world. They have never grown up."

The same phenomenon of neoteny is responsible for the retention of the sutures between the bones of the skull in the ostrich. In the Carinates, the sutures between the bones are present in the young stages, but they are obliterated in the adult skull, which is a structure of great solidity, in all probability adapted to the necessity for withstanding the mechanical stresses consequent upon active flight. In retaining the sutures between the bones of the skull the ostrich, having lost the power of flight, shows a secondary return to the juvenile condition of the ancestral flying bird, and, of course, the ancestral reptile.

The inclusion of the dromaeognathous or palaeognathous palate among the neotenous features of the Ratites, with the implication that it is the result of a secondary retention of an ancestral juvenile condition, may appear surprising in view of the selection of this very structure by T. H. Huxley as the basis for his classification of birds, and his view that the dromaeognathous type was primitive. Nevertheless, the evidence is quite clear, as W. P. Pycraft (1900, 1901) has shown, although he did not realize its significance. The so-called palaeognathous palate is an arrested stage in the development of the neognathous palate. Precisely the same conclusion was reached by S. McDowell (1948) on other grounds, namely the impossibility of giving a definition of the palaeognathous palate applicable to all Ratites and tinamus and excluding all Carinates (except tinamus) because of its great variation.

The essential feature of Huxley's dromaeognathous and Pycraft's paleognathous palate is the fact that the pterygoids extend forwards and make contact with the hinder ends of the prevomers, while the palatines lie further to the side. In Huxley's schizognathous and aegithognathous types, or Pycraft's neognathous palates, the usual condition in the adult is that the pterygoids do not make contact with the prevomers, but are separated from them by the palatines with which the pterygoids make a joint. But Pycraft's remarkable discovery, to which insufficient attention has been paid, was that in the development of many " neognathous " birds the palate passes through a " palaeognathous " stage in which the pterygoids actually or nearly come into contact with the prevomers ; but the anterior ends of the pterygoids then become detached from the remainder of these bones, and, instead, become attached to the hinder ends of the palatines, where they give rise to the so-called " mesopterygoid " elements of W. K. Parker (1875, 1876, 1877, 1879), and the " hemipterygoid " of Pycraft. Between the detached anterior portion and the remainder of the pterygoid a joint is formed. This is why in the adults of these birds the pterygoid seems not to reach the prevomer, whereas morphologically, in fact, it does or almost does reach it. The hemipterygoid in various Carinates is shown in Plates 8 and 9 for comparison with the conditions in Ratites.

For those, if there be any, who still believe in the theory of recapitulation, it would no doubt be tempting to say that the neognathous palate " recapitulates " in its development the condition of the palaeognathous palate which would therefore be ancestral. But in view of the overwhelming evidence that the Ratites are secondarily descended from flying birds, the fact that the Ratites already show neoteny in two other features, the plumage and the bones of the skull, and the probability, from A. Kleinschmidt's (1951) reconstruction, that the palate of *Archaeopteryx* was neognathous (schizognathous), it is impossible to believe that in their palates the Ratites are primitive. The palaeognathous type of palate must therefore be neotenous. This means a complete reversal of the hitherto generally held view of the palate of birds and necessitates the conclusion that the so-called neognathous palate is primitive.

The primitive nature of the neognathous palate in birds is probably connected with the phenomenon of kinetism. J. Versluys (1910) has shown that the mesokinetic condition in Carinates, where the quadrate and pterygoid bones are capable of a certain amount of movement and sliding, and there is a joint between the pterygoid and palatine whereby the upper jaw can be moved on a hinge at the level of the lacrimal bones and raised relatively to the brain-case, is only intelligible if the birds were evolved from reptiles in which a similar though less extensive power of movement was possible : the condition which he has called metakinetic. According to him (1910 : 244) even *Archaeopteryx* had a kinetic skull capable of movement, although it still possesses a preorbital bar separating the preorbital fossa from the orbit, and a suborbital bar. But in the Ratites the power of movement has been reduced ; the quadrate has a broad connexion with the pterygoid, the latter has equally broad connections with the palatines and the prevomer, and there is no movable joint between the pterygoid and the hemipterygoid because these two elements have not become separated. It must be concluded therefore that with the loss of flight, general increase in size, and acquisition of different feeding habits, the Ratites have lost the Carinates' power of movement of the upper jaw, by retaining the juvenile condition of the palate before any joint is formed. I am greatly indebted to Dr. W. C. Osman Hill for informing me that even in the kiwi, which is the smallest of the Ratites, there is no mobile joint at the base of the upper jaw ; and that in the cassowary the only very slight mobility in the upper jaw is at a point far forward, just behind the nostrils.

Further, there is a curious point in the distribution of the palaeognathous type of palate among the birds. It is found not only in Ratites, but also in the tinamus, which are Carinates with a well-developed keel on the sternum and good power of flight. This fact in itself is sufficient to indicate that the Ratites have lost the power of flight, for it could hardly be contended that the tinamus have evolved flight from a flightless Ratite condition.

As for the argument that the absence of any rudiment of the clavicle in the ostrich implies that it was evolved from ancestors which lacked the clavicle (and, by implication, could not fly), it is another example of the fallacies to which the theory of recapitulation leads by its assertion that early embryonic stages of development must represent early ancestral stages in evolution. Modern birds lack even the rudiments of teeth, but teeth are present in *Archaeopteryx*, *Hesperornis*, and *Ichthyornis*. The absence of tooth rudiments in modern birds no more excludes *Archaeopteryx* from their ancestry than the absence of limb-rudiments in snakes indicates that their ancestors were limbless.

Finally, the embryonic development of the emu, studied by H. Steiner (1936) and H. Lutz (1942), shows that the structure and organization of the Ratite embryo is so similar to the Carinate that it can only be interpreted on the view that Ratites have evolved from flying birds.

CONCLUSIONS

On all these grounds, therefore, there can be no doubt that Owen was correct in regarding the Ratites as birds which have " abrogated " the power of flight. It is possible to go further and to say that they have degenerated from a Carinate condition. Whether the Ratites represent a natural group or whether they are an assemblage of forms which have independently followed parallel lines of evolution consequent on the loss of flight is a further problem for ornithologists to solve.

In view of the incontrovertible evidence from the structure of the wing, the pygostyle, and the cerebellum, that the Ratites have degenerated from flying birds, any attempt to explain the persistent juvenile characters of the Ratites (nestling-down, skull-sutures, and palate) as phylogenetically primitive is doomed to failure ; and the Ratites must be regarded as providing one of the most telling exposures of the fallacy of the theory of recapitulation.

I am glad to acknowledge the help of my colleagues in the Bird Room of the British Museum (Natural History), Mr. J. D. Macdonald and Miss P. A. Lawford, of Dr. W. E. Swinton of the Department of Geology, and of Mr. J. V. Brown, Senior Photographer.

SUMMARY

Now that the anatomy of *Archaeopteryx* is adequately known, it is possible to make a rigorous analysis of the characters of the Ratites in the light of the conditions shown by primitive birds. The structure of the wing, tail, and brain in Carinates shows advances on *Archaeopteryx* which are undoubtedly adaptations to flight. The presence of the same features in Ratites proves that they are descended from flying birds. The condition of the plumage, the sutures between the bones of the skull, and the disposition of the bones of the palate in Ratites, all show secondary retention of characters which are juvenile in Carinates, and are evidence of neoteny in the Ratites.

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EXPLANATION OF PLATES

PLATE 5

(1) Right side view of the pygostyle in a Carinate, *Leptoptilos crumeniferus* (Marabou Stork) and (2), in a Ratite, *Struthio camelus*, showing the similarity of structure. (ap), the anterior portion showing the elements of a distinct vertebra; (pp) posterior portion composed of fused vertebrae.

PLATE 6

(1) The brain as seen in right-side view in *Archaeopteryx lithographica*. (2) sagittal section of the brain in a Carinate, *Tringa ocrophus* (Green Sandpiper), and (3) in a Ratitie, *Rhea americana*. (ce), cerebellum; (ch), cerebral hemisphere; (ol), optic lobes.

PLATE 7

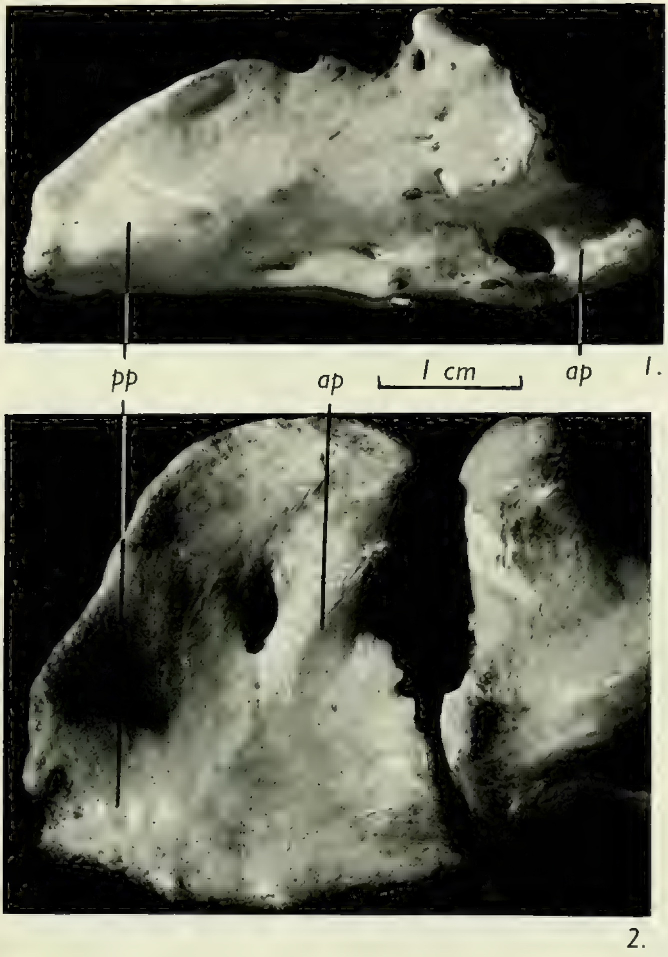
The arrangement of the feathers on the wing of a young Ratite, *Rhea americana*, showing the differentiation between primary and secondary remiges, bastard wing, and wing-coverts.

PLATE 8

(1) Ventral view of the structure of the palate in the Carinate *Pygoscelis papus* (Gentoo penguin) nestling; (2) in the Carinate *Anthropoides paradisea* (blue crane); and (3) in the Ratite *Dromiceus novae-hollandiae* (emu). (hpt), hemipterygoid; (pa), palatine; (pt) pterygoid; (pr), prevomer; (qu), quadrate.

PLATE 9

(1) The structure of the palate as seen in left-side view in *Corvus frugilegus* (rook) young; (2), *Megalaema* virens (Himalayan barbet). (hpt), hemipterygoid; (ju), jugal; (pa), palatine; (pt), pterygoid; (pr), prevomer; (qu), quadrate.



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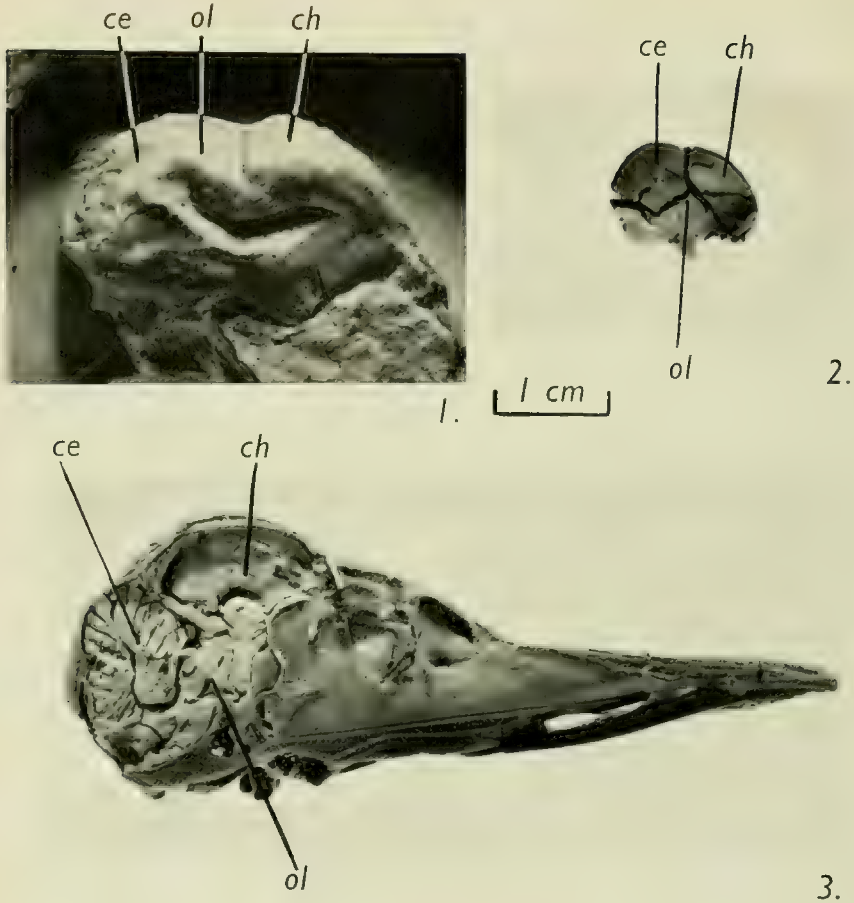

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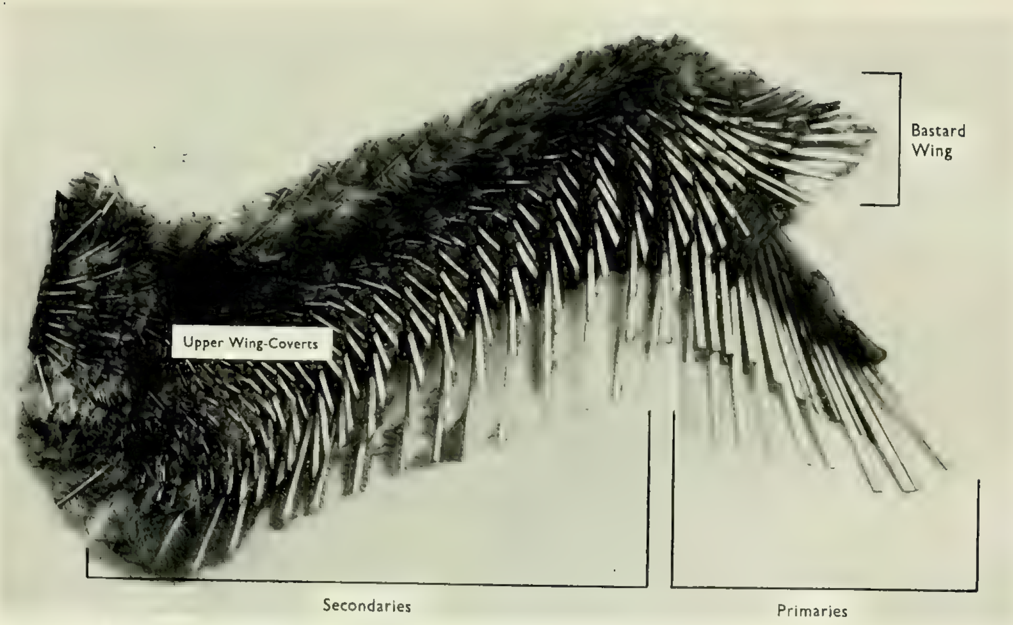
Bastard Wing
Upper Wing-Coverts
Secondaries
Primaries

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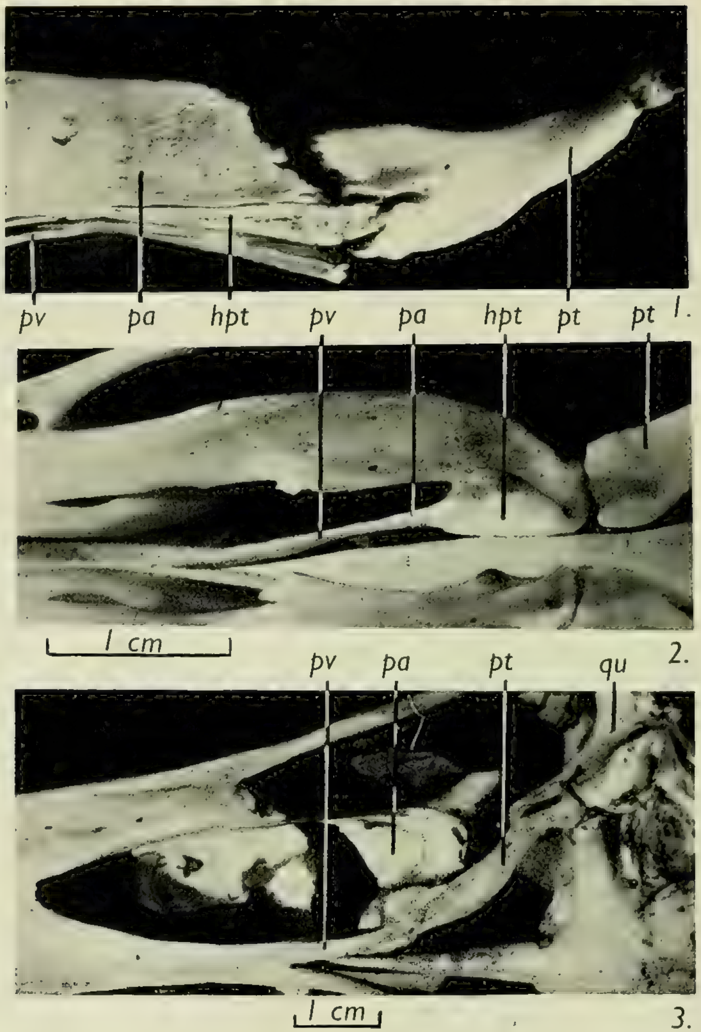
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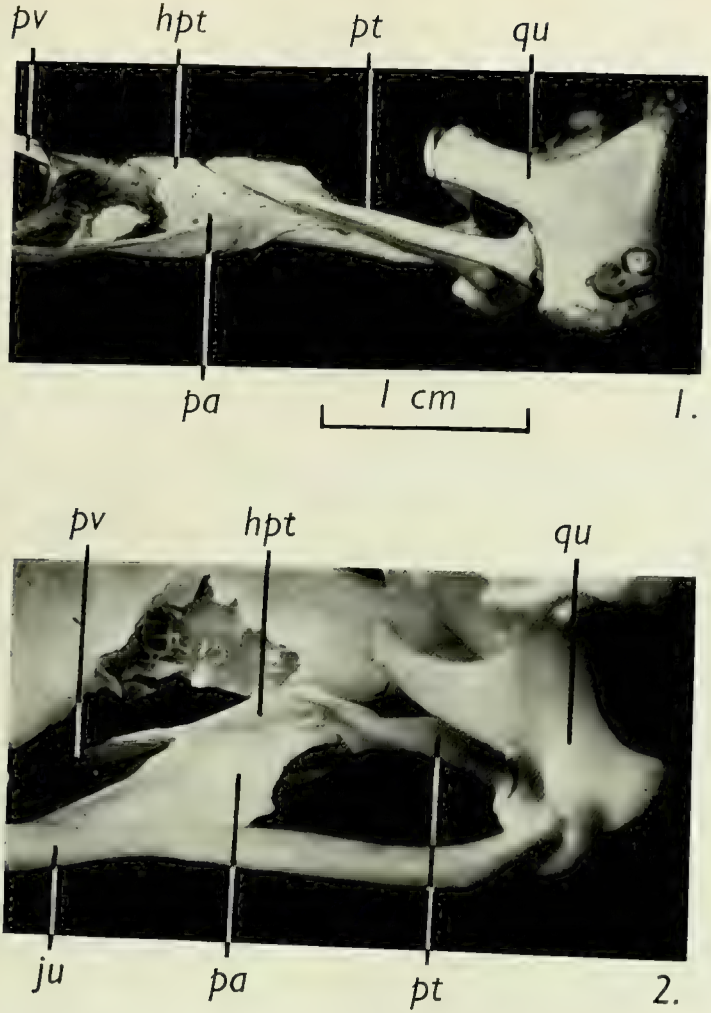
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STUDIES ON THE TRICHIUROID FISHES—3

A PRELIMINARY REVISION OF THE FAMILY TRICHIURIDAE

BRITISH MUSEUM NATURAL HISTORY

DENYS W. TUCKER

BULLETIN OF
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STUDIES ON THE TRICHIUROID FISHES—3[1]

A PRELIMINARY REVISION OF THE FAMILY TRICHIURIDAE

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SYNOPSIS

This paper presents a working classification of the Trichiuridae, based on a consideration of the literature of the family and examination of selected material, which has been prepared as a prelude to Reports on the "Dana" collections of Trichiuridae and Gempylidae. Three subfamilies are recognized : Aphanopodinae (genera *Diplospinus, Aphanopus, Benthodesmus*) ; Lepidopodinae (genera *Lepidopus, Evoxymetopon, Eupleurogrammus, Assurger, Tentoriceps*) and Trichiurinae (genera *Trichiurus, Lepturacanthus*). Keys, diagnoses and synonymies are presented and figures given of all species recognized. *Diplospinus* is considered to be the most primitive genus extant and grounds are given for relating it to the Gempylid *Nesiarchus*. The origin and radiation of the Trichiuridae are discussed.

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[1] The previous papers in this series were : (1) The fishes of the genus *Benthodesmus* (Family Trichiuridae), *Proc. zool. Soc. Lond.* **123** : 171–197, 3 pls., 5 text-figs. (1953). (2) *Benthodesmus tenuis* (Günther) collected by the Expédition Océanographique Belge dans les eaux côtières de l'Atlantique Sud (1948–1949), with additional notes on the genus *Benthodesmus, Bull. Inst. roy. Sci. nat. Belg.* **31**, No. 64 : 1–26, 1 pl., 11 text-figs. (1955).

INTRODUCTION

As I contemplated the mass of material which resulted from my rash acceptance of Dr. Anton Fr. Bruun's invitation to write reports on the young Trichiuroid fishes collected by the "Dana" Expeditions, I realized the urgent need of some preliminary working classification with which to regulate the chaos that must ensue once these many thousands of specimens were released, like so many djinns, from their tubes and bottles.

The problem of the Gempylidae was immediately relieved by Matsubara and Iwai (1952) and by Mrs. Marion Grey (1953), but the case of the Trichiuridae remained desperate. There has been no comprehensive revision of this family since the end of the nineteenth century. The earlier synopses of Günther (1860), Gill (1863) and Goode and Bean (1895) are no longer adequate accounts even of the genera which they describe and, moreover, contain no attempt at a phyletic classification since they date from a period before the planting of family trees became fashionable. Later workers have had varying success in distinguishing the genera and species of limited regions. In this century a few new species and genera have been proposed, two of the latter without any of the inhibitions consequent upon an interest in the family or the possession of study-material.

The present draft revision assigns a place to every nominal genus and species and gives, as a minimum, the reference for the first publication of every name and name-combination, together with selected items from the remaining literature. It gives diagnoses and a phyletic classification of all sub-families, genera and species recognized and argues the case for synonymies with whatever detail the individual circumstances may immediately demand. Except for *Evoxymetopon*, *Assurger* and *Tentoriceps* (of which material or new published descriptions would be greatly appreciated), material of all genera and species has been examined, including a substantial number of type specimens.

The author of any "preliminary" contribution should justify his title. The amount of labour involved in preparing the present MS as a working tool has shown the need of such a tool and of certain small but critical contributions to the understanding of the Trichiuridae which those possessing rarer material may make. It will be some considerable time before the final "Dana" Reports on the Trichiuridae and Gempylidae can be completed and so, *faute-de-mieux*, a preliminary account appears likely to be useful, even though some of its conclusions may be subject to second thoughts.

I wish to express my thanks to Messrs. P. E. Purves and A. C. Wheeler of the British Museum (Natural History) for numerous radiographs which have been of very great assistance in this work.

THE CHARACTERS OF THE FAMILY TRICHIURIDAE

Regan (1909) allies the Trichiuridae with the Gempylidae as the Trichiuriformes, forming the first division of his suborder Scombroidei of the order Percomorphi. He characterises the Trichiuriformes as having :—

> "Caudal fin-rays not deeply forked at the base, the hypural in great part

> exposed. Praemaxillaries beak-like, free from the nasals; mouth toothed, with lateral cleft; strong anterior canines. Epiotics separated by supraoccipital. Gill-membranes free from the isthmus. Pectoral fins placed low."

With this diagnosis I have no present disagreement save to comment that hypurals are sometimes absent and to prefer the use of "fangs" or "caniniform teeth" rather than "canines" for fish teeth; the term "canine" is best restricted to certain reptiles and to the mammals, in which it is defined, not by form but by position and homology, as "the most anterior tooth of the maxilla, situated on or immediately behind the premaxillo-maxillary suture . . . or the tooth in the lower jaw which bites in front of the upper canine".

Regan's diagnosis of the family Trichiuridae follows:

> "Body very elongate, strongly compressed; maxillary sheathed by the praeorbital; spinous dorsal, if distinct, not longer than the soft[1]; anal with numerous short spines[2]; pelvic fins reduced to a pair of scale-like appendages or absent[3]; caudal small or absent. Dorsal and anal rays corresponding to the vertebrae[4], each interneural or interhaemal attached to a neural or haemal spine; pelvic bones, if present, united to form a slender spicular bone connected with the cleithra by a long ligament[5]. Vertebrae numerous, 100(43 + 57) to 159(39 + 120) or more[6]; ribs feeble, sessile."

This description is evidently based primarily upon examinations of *Lepidopus*, *Aphanopus* and *Trichiurus* and requires several modifications and qualifications:

(1) The spinous dorsal is always distinct; it is longer than the soft in *Diplospinus* (discovered since Regan's time) and very slightly longer than the soft in occasional specimens of *Aphanopus*.

(2) Some, if not all, of the anal rays are split, soft and support a fin-membrane (*Diplospinus*, *Aphanopus*, *Benthodesmus*, *Lepidopus*, *Evoxymetopon*, *Assurger*); in *Trichiurus*, *Lepturacanthus* and *Eupleurogrammus*, however, the anal rays are much reduced spinules or entirely absent. At the origin of the anal fin, moreover, immediately behind the vent, are two spines (represented by the notation i + I throughout the present paper); of these the anterior is a minute spinule while the second may be variously enlarged as a leaf-like or keeled scute, or as a stout spine.

(3) The pelvic fins in some genera (*Diplospinus*, *Aphanopus*, *Benthodesmus*, *Lepidopus*) and probably in all in which they are present, consist each of a scale-like spine and one rudimentary soft ray, the latter newly noticed.

(4) The dorsal spines and their basals and interneurals always correspond to the trunk vertebrae; the dorsal soft rays may be twice as numerous as the adjacent vertebrae (*Diplospinus*), slightly more numerous (*Aphanopus*, *Benthodesmus*) or as numerous (remaining genera).

(5) The pelvic bones form an imperfectly fused, fenestrated structure which is not always elongated.

(6) The vertebrae range from 34 + 24 = 58 (*Diplospinus*) to 53 + 103 = 156 (*Benthodesmus simonyi*) or 41 + 151 = 192 (*Eupleurogrammus muticus*).

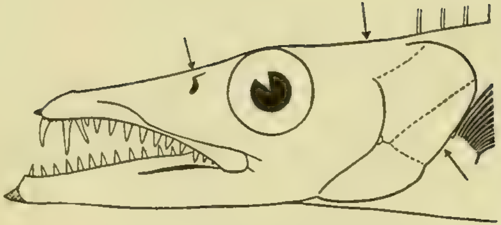

FIG. 1.—A typical Aphanopodine head (*Aphanopus*). There is no elevation of the ethmo-frontal region; the posterior confluence of the frontal ridges does not form a crest; the free margin of the subopercular is convex.

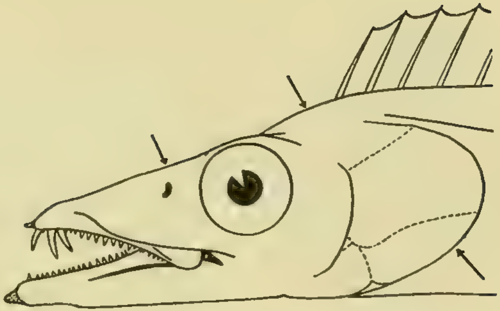

FIG. 2.—Types of Lepidopodine head: *Lepidopus*. The posterior confluence of the frontal ridges is elevated to form a sagittal crest, which is, in this form, however, confined to the nape. The free margin of the subopercular is convex.

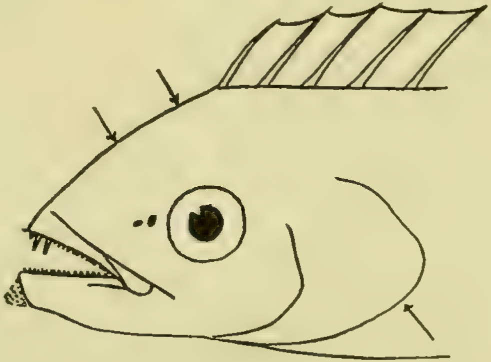

FIG. 3.—Types of Lepidopodine head: *Evoxymetopon* (re-drawn after Goode & Bean). The posterior confluence of the frontal ridges is elevated to form a sagittal crest, which is continued forward along the snout as an elevation of the entire ethmo-frontal region. The free edge of the subopercular is convex.

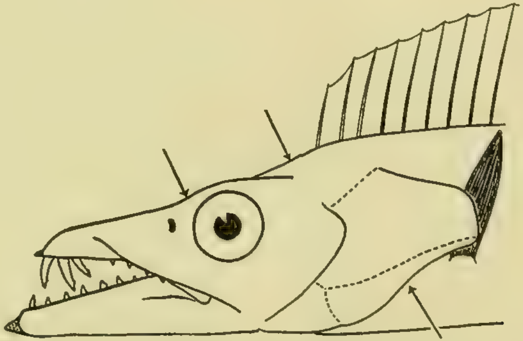

FIG. 4.—A typical Trichiurine head (*Trichiurus*). The posterior confluence of the frontal ridges is elevated to form a sagittal crest, which, in this subfamily, is confined to the nape. The free margin of the subopercular is concave.

A SHORT KEY TO THE SUBFAMILIES AND GENERA OF THE FAMILY TRICHIURIDAE

Frontal ridges not elevated, no sagittal crest. Profile of head rising very gently from
  snout tip to dorsal (cf. Text-fig. 1) . . . . . . APHANOPODINAE (p. 77)
  D.72–73. Spinous dorsal base twice as long as soft . . . . *Diplospinus* (p. 78)
  D.82–87. See "*Lepidopus xantusi*" (Lepidopodinae)
  D.91–95. Spinous and soft dorsal bases sub-equal . . . . . *Aphanopus* (p. 81)
  D.120+ Spinous dorsal base half as long as soft . . . . *Benthodesmus* (p. 85)
Posterior confluence of frontal ridges elevated, forming a prominent sagittal crest at the
  nape, which may or may not be continued forward as a ridge-like elevation of the
  ethmo-frontal region (cf. Text-figs. 2, 3 and 4).
  Ventral fins present. Lateral line descending gently from the shoulder and median or
    sub-median along the body, i.e. distance from lateral line to ventral profile at
    anus much more than half distance from lateral line to dorsal. Lower hind
    margin of operculum convex . . . . LEPIDOPODINAE (p. 89)
    Sagittal crest confined to nape. Interorbital concave. Caudal present
      Lepidopus (p. 90)
    Sagittal crest continuous from snout tip to dorsal. Interorbital convex
      Caudal present
        D.87–93. Body depth 12–13 in length . . . . . *Evoxymetopon* (p. 97)
        D.120. Body-depth 20–28 in length . . . . *Assurger* (p. 106)
      Caudal absent.
        Body depth 14–18 in length . . . . . . *Eupleurogrammus* (p. 102)
        Body depth 20–24 in length . . . . *Tentoriceps* (p. 110)
  Ventral fins absent. Lateral line descending steeply from the shoulder and running
    near the ventral profile of the body, i.e. distance from lateral line to ventral profile
    at anus less than half distance from lateral line to dorsal. Lower hind margin of
    operculum more or less concave. Caudal always absent (cf. Text-fig. 4)
      TRICHIURINAE (p. 112)
    Post-anal scute small, less than the pupil. Soft anal rays not breaking through
      skin. Eye large, 5.0–7.0 in head . . . . . . *Trichiurus* (p. 113)
    Post-anal scute large, half the eye-diameter. Soft anal rays pungent spinules,
      breaking ventral profile. Eye small, 6.7–10.0 in head . . *Lepturacanthus* (p. 119)

SYSTEMATIC REVIEW

Subfamily APHANOPODINAE Gill

Aphanopodinae Gill, 1863, *Proc. Acad. nat. Sci. Philad.* **1863** : 225.

Type genus *Aphanopus* Lowe.

GENERA NOW RECOGNISED.—*Aphanopus* Lowe ; *Benthodesmus* Goode & Bean ; *Diplospinus* Maul.

DIAGNOSIS :

A. Snout gently sloping ; orbits entering upper profile of head ; frontal ridges only slightly elevated, not contributing to a sagittal crest.

B. A stout, conical, cartilaginous protuberance at the mandibular symphysis ; another, much smaller, at the tip of the snout.

C. Lower hind margin of operculum markedly convex.

D. Teeth of main series with double barbs (*Diplospinus*) or entirely without barbs (*Aphanopus, Benthodesmus*).

E. Teeth on palatines in a linear series. (In *Aphanopus* only 1–2 posterior rudiments of the series present.)

F. Lateral line descending gently from the shoulder and running in a median or sub-median position along the body, i.e. distance between lateral line and ventral profile much more than half distance between lateral line and dorsal.

G. Spinous dorsal fin long, with 32–46 rays. Spinous and soft dorsals partly divided by a slight notch.

H. Soft dorsal rays slightly more numerous than adjacent caudal vertebrae, or up to twice as many. Basal and interneural elements intercalated among the main series and unrelated to neural spines of vertebrae.

I. Spinous anal i + I ; anterior soft anal rays weak but (except in *Benthodesmus simonyi*) an external fin is continuous in some form or other from the vent nearly to the caudal ; the properly developed fin may extend the whole length or be confined to the posterior 20–25 rays.

J. Terminations of dorsal and anal fins sub-opposite.

K. Caudal fin always present ; small, normal, forked.

L. Ventral fins always present (though reduced to internal rudiments in adult *Aphanopus*), composed each of a scale-like spine and one soft ray ; in the adult fish inserted not more than 2–3 mm. before/behind anterior/posterior perpendiculars through the ends of the pectoral base.

M. Pyloric caeca few (6–9) ; (not verified in *Diplospinus*).

Osteological Literature

Günther, 1860, *Cat. Fish. B.M.* **2** : 342–344 (desc. osteology *Aphanopus*).

Tucker, 1953, *Proc. zool. Soc. Lond.* **123** : 196–197, pls. 2–3 (figs. osteology of paired fins and anal fin of *Aphanopus & Benthodesmus*).

—— 1955, *Bull. Mus. Hist. nat. Belg* **31,** No. 64 : 1-26 (figs. osteology of pelvic and anal fin of *Benthodesmus*).

Literature on young stages

Maul, 1948, *Bol. Mus. Funchal* No. **3,** Art **6** : 42, fig. 17 (young *Diplospinus*).

Tucker, 1953, *op. cit.* : 187 (figs. young *Aphanopus* and *Benthodesmus*).

Genus ***DIPLOSPINUS*** Maul

Diplospinus Maul, 1948, *Bol. Mus. Funchal* No. **3,** Art. **6** : 42.

Type species *Diplospinus multistriatus* Maul. Monotypic.

Synonyms

Lepidopus (*non* Gouan 1770) (part) Brauer, 1906.

Benthodesmus (*non* Goode & Bean 1882) (part) Goode & Bean, 1895 ; Fowler, 1938. (Refs. below.)

Diagnosis :

(1) Body elongate, head length 6·6–6·9 in standard length 125–203 mm., body depth 18·5 in S.L.

(2) Vent exactly in middle of S.L.

(3) Vertebrae 34 + 24 = 58. (Corresponds to 36 + 22 = 58 in convention used for *Benthodesmus.*)

(4) Spinous dorsal base twice as long as soft dorsal base.

(5) Dorsal spines 32–33 ; dorsal soft rays 40.

(6) Dorsal soft rays about twice as numerous as adjacent caudal vertebrae, so that alternate interneural elements do not articulate with neural spines.

(7) Anal spines i + I, the former half the length of the latter in young stages ; condition in the adult unknown ; i is linear ; I is dagger-shaped and V-shaped in transverse section.

(8) Anal spines i and I articulate close together on a common basal, which is not enlarged or specially modified and which, except that it does not quite touch the corresponding haemal arch, does not show any difference in the size and relations of the interhaemal process from those which follow it. (Condition similar to *Lepidopus.*)

(9) A complete external anal fin supported by 31 split but unbranched rays extending from the spinous anal nearly to the caudal. The soft rays and their basal elements are about twice as numerous as the adjacent caudal vertebrae, so that alternate basals have interhaemal processes which are unrelated to haemal arches.

(10) Ventral fins inserted on perpendicular through anterior end of pectoral fin-base.

(11) Ventral fin I–1 ; a narrow scale-like spine and an external split ray twice as long.

(12) All principal teeth of the premaxillary and dentary series are strongly barbed (arrowhead-shaped), with thickened enamel caps.

(13) Palatine teeth in a linear series, exposed.

(14) Principal teeth on first gill-arch numerous.

(15) Long intermuscular (pleurals and epipleurals) bones present, extending throughout trunk.

(16) Melanophores distributed in parallel and narrow longitudinal rows along the body.

One species, *Diplospinus multistriatus* Maul, Atlantic and Indo-Pacific.

Diplospinus multistriatus Maul,

(Text-fig. 5)

Benthodesmus atlanticus (part) Goode & Bean, 1895, *Oceanic Ichthyology* : 206 (the two small specimens mentioned, *fide* Dr. Carl L. Hubbs, *in litt.*).

Benthodesmus benjamini (part) Fowler, 1938, Proc. U.S. Nat. Mus. **85** : 45 (certain of the paratypes, *fide* Dr. Carl L. Hubbs, *in litt.*).

? *Lepidopus gracilis* Brauer, 1906, *Wiss. Ergeb.* " *Valdivia* " **15** : 291, Taf. XII, fig. 1 (not fig. 5 as erroneously stated in the text nor fig. 3 as stated in the legend to the plate).

Holotype in the Berlin Museum ? Type locality West coast of S. Africa, St. 82. 21° 53′ S., 6° 58′ 6″ E.

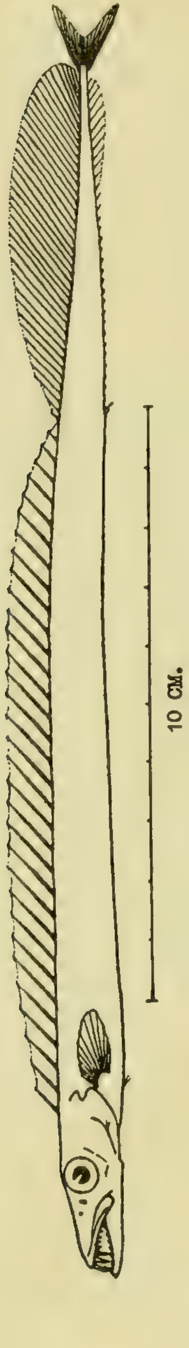

FIG. 5.—*Diplospinus multistriatus* Maul. Holotype, 203 mm. S.L. (After Maul, 1948; altered.)

Diplospinus multistriatus Maul, 1948, *Bol. Mus. Funchal*, No. **3**, Art 6 : 42, fig. 17.
Holotype Museu Municipal do Funchal No. 3063. Type locality Madeira.
Paratypes Museu Municipal do Funchal Nos. 3064–5, 3067–9.
Paratype British Museum (Natural History) No. 1953.10.28.1. (Formerly 3066.)

Certain discrepancies will be noticed between the generic diagnosis given above and the otherwise accurate description and figure by Maul (1948) ; the corrected observations have been made on the paratype kindly presented by Mr. G. E. Maul. Each ventral fin includes a soft ray in addition to the spine ; there is a single row of about a dozen teeth on each palatine (" no teeth on vomer or palatines ") ; there are traces of an apparent and highly probable lateral line (" no lateral line ") though the present specimen is completely skinned ; certain of the premaxillary fangs are represented by replacement teeth (" depressible teeth "). The number of branchiostegal rays is 7, as in other Trichiurids. The number of pyloric caeca cannot be determined owing to destruction of the thoracic region. There is a deep notch on the hinder margin of the opercular, as already observed by Maul, and this character proves to be rather important since it is confined to *Diplospinus*, the most primitive recent Trichiurid and to *Nesiarchus*, the nearest-related Gempylid (see p. 124).

Since Brauer's (1906) figure of *Lepidopus gracilis* bears the magnification 2/1 we may deduce a S.L. of 68 mm., i.e. about one-third the length of the type series of *Diplospinus multistriatus*. The head is 4·8 and the height 14·4 in the length ; the eye goes 5 times in the head, and the ventral and anal spines are proportionately longer than in the types. All these differences are in the directions to be expected in a younger fish. The counts of D.65–67 and A.27 are slightly low, but not outside the probable range of variation or error. However, the eye is shown about a quarter its diameter *below* the dorsal profile of the head, the origin of the dorsal fin is a little retarded and the insertion of the ventral fins is below the posterior rather than the anterior end of the pectoral base (" Bauchflosse kurz hinter der Vertikale der Brustflosse "). These discrepancies must await a satisfactory explanation, which is likely to result in *Diplospinus gracilis* (Brauer) becoming the definitive name of the present species.

Genus ***APHANOPUS*** Lowe

Aphanopus Lowe, 1839, *Proc. zool. Soc. Lond.* **7** : 79.

Type species *Aphanopus carbo* Lowe. Monotypic.

Synonyms

Lepidopus (*non* Gouan, 1770) Sim, 1898 ;Dons, 1921. (Refs. below).

DIAGNOSIS :

(1) Body elongate, head length 5·68–4·92 in standard length 102–1036 mm., body depth 21·7–11·23 in same.
(2) Tail 48–49% of standard length.
(3) Vertebrae 42–44 + 55–56 = 98–99.
(4) Spinous and soft dorsal bases sub-equal, differing by at most ± 3 % of S.L.
(5) Dorsal spines 38–41 ; dorsal soft rays 53–56 ; aggregate 91–95.
(6) Dorsal soft rays practically corresponding with adjacent caudal vertebrae.

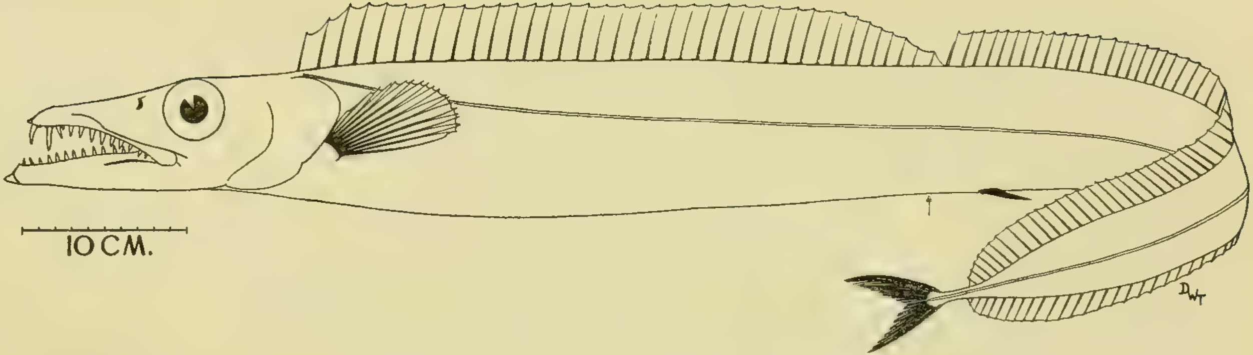

FIG. 6.—*Aphanopus carbo* Lowe. Holotype, 1,012 mm. S.L.

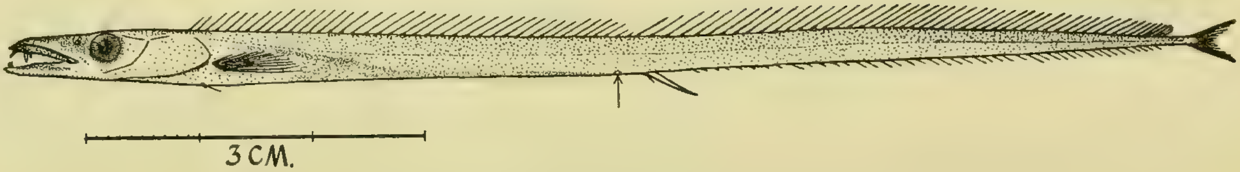

FIG. 7.—*Aphanopus carbo* Lowe, juvenile 102 mm. S.L. (Holotype of *A. acus* Maul, after Maul (1948), altered from the specimen.)

There are very few intercalated interneural elements which are unrelated to neural spines and these occur usually towards the beginning and end of the fin.

(7) Anal spines i + I, the former about 1/5 the length of the latter in the young stages but becoming disproportionately smaller in the adult, in which i becomes a minute sharp spinule, usually concealed beneath the skin and I is a stout dagger-shaped spine, triangular in cross-section.

(8) Anal spine i articulates a short distance in advance of I. Their common basal element is a complex, greatly enlarged and strengthened to accommodate the hypertrophied I, and representing four or more fused elements. The compound interhaemal process is stout and does not touch the adjacent haemal arch. The horizontally directed component of the compound basal element occupies the length of three vertebral centra and the presumed anterior migration of the corresponding interhaemal processes leaves a space above it.

(9) A complete external anal fin of 44–48 split but unbranched rays extending from the spinous anal nearly to the caudal. The anterior rays are very weak and the functional fin is effectively confined to the posterior 20–25 rays. The internal supporting skeleton is quite regular ; there is a precise correspondence between rays, basal elements and caudal vertebrae, with a close association between interhaemal processes and haemal arches.

(10) Ventral fins inserted immediately before perpendicular through anterior end of pectoral fin-base. External fins present only in the juvenile ; fins and girdle reduced to an internal rudiment in the adult.

(11) Ventral I–1 in the juvenile only ; a narrow spine and an external split ray initially about 3 times as long.

(12) Principal teeth of the premaxillary and dentary series without barbs : if these are sometimes present on the premaxillary fangs they are usually barely perceptible and confined to the hinder edges, without enamel thickening. The marginal teeth of the jaws are stout, triangular and have microscopically-serrated edges.

(13) Palatine teeth reduced to 1–2 minute rudiments at hinder end of bone, very much concealed.

(14) Principal teeth on first gill-arch very numerous.

(15) Intermuscular bones (pleurals and epipleurals) weaker than in *Diplospinus*.

(16) Pigmentation uniform, dense ; fish uniform black when dead. Living fish coppery with iridescent reflexions.

One species, *Aphanopus carbo* Lowe, N. Atlantic and Gulf of Aden.

Aphanopus carbo Lowe

(Text-figs. 6 & 7).

Aphanopus carbo Lowe, 1839, *Proc. zool. Soc. Lond.* **7** : 79.

Holotype B.M. (N.H.) No. 1851.11.29.6. Type locality Madeira.

Aphanopus minor Collett, 1886, *Chr. Vid.-Selsk. Forh.* **1886** No. 19 : 1, fig. 1.

Holotype in Universitetets Zoologiske Museum, Oslo. Type locality Denmark Strait, E. of Greenland, 65° N., 31° W.

Lepidopus caudatus (*non* Euphrasen, 1788) Sim, 1898, *Ann. Scot. nat. Hist.* **1898** : 53.

Aphanopus schmidti Saemundsson, 1907, *Vid. Medd. naturh. Foren. Kbh.* **59** : 22, Pl. 1.

Holotype in Náttúrugripasafnid, Reykjavík.

Paratype B.M. (N.H.) No. 1925.7.23.4. Type locality Vestmann Is., S.W. of Iceland.

Lepidopus atlanticus (*non* Goode & Bean, 1895) Dons, 1921, *Tromso Mus. Aarsh.* **43**, No. 6 : 10, fig. 1.

(Identification corrected to *Aphanopus schmidti* by Soot-Ryen, 1936, *Nytt. Mag. Naturv.* **76** : 237.)

Aphanopus microphthalmus Norman, 1939, *Sci. Rep. John Murray Exped.* **7** No. 1 : 71, fig. 25.

Holotype B.M. (N.H.) No. 1939.5.24.1322. Type locality Gulf of Aden.

Aphanopus acus Maul, 1948, *Bol. Mus. Funchal* No. **3**, Art. 6 : 47, fig. 18.

Holotype in Museu Municipal do Funchal. Type locality Madeira. (Withdrawn as young *A. carbo* by Maul, 1949, Bol. Mus. Funchal, No. **4**, Art. 10 : 21.)

non Aphanopus simonyi Steindachner, 1891. (See under *Benthodesmus simonyi.*)

non Aphanopus carbo Norman, 1937. (Mediterranean records based on confusion with *Lepidopus caudatus*, q.v.)

TABLE I.

Holotype.	Vertebrae.	Dorsal.	Anal.
A. carbo	42+56	XXXVIII, 56	i+I+48
A. schmidti	42+56	XXXVIII, 55	i+I+46
A. minor	44+ ?	XLI, ?	i+I+ ?
A. microphthalmus	44+55	XLI, 54	i+I+45

In the type of *A. minor* the tail has been broken off a short distance behind the vent and has subsequently healed over with some slight re-orientation of the soft dorsal and anal rays remaining. The remnant includes 25 caudal vertebrae, 28 soft dorsal rays, 21 anal elements.

Through the kindness of Dr. C. Støp-Bowitz (Oslo), Dr. Finnur Gudmundsson (Reykjavík) and Mr. G. E. Maul (Funchal) I have been able to examine the types of all the nominal species of *Aphanopus* and, by comparing these with a series of some thirty specimens from the type locality and as many more from the North Atlantic, to decide that they represent only one species, *A. carbo* Lowe.

A. acus Maul is a juvenile *A. carbo* and has already been adequately dealt with by Maul (1949). Meristic counts for the other nominal species are given in Table I. Ranges of vertebral counts for the long series are not yet available. but the variations now tabulated are small and well within the limits of those found in *Benthodesmus tenuis* (p. 88). Fin-ray counts on eighteen Madeiran specimens give ranges D.XXXVIII–XL, 53–55 (aggregate 91–95) ; A. i + I + 44–48.

The validity of *A. schmidti* has been much debated, Saemundsson *pro*, Grieg and others *con*. The arguments will be dealt with in detail elsewhere ; for the present it is sufficient to state that the two specimens of *A. schmidti* show no meristic differences from *A. carbo* nor any measurable differences in body proportions. The shorter dorsal rays noted by Saemundsson are merely broken ; the intangible differences in the contour of the head are due to variations of desiccation and fixation, and may be observed in some of the fishes on the Funchal Market slabs ; the colour described with poetic exactitude by Saemundsson is merely that of a living *A. carbo* and changes to a glossy black as a post-mortem effect.

A. minor Collett is founded on a wretched half-grown fish which had somehow contrived to survive the loss of its tail. I have compared the holotype with a Madeiran specimen of equivalent snout-vent length ; there are no differences.

A. microphthalmus Norman has been checked against a similar-sized specimen from Madeira ; there are no significant differences. The distension of the branchiostegal region of the holotype, adequately shown in Norman's figure. gives an exaggerated superficial impression of a deeper head and smaller eye.

Sim (1898) compares a Scottish fish with Day's description of *Lepidopus caudatus* and comments :

> " Now in the specimen under notice there is not the slightest indication of such ventral scales, and what is considered a scale by the authors named takes the form of a strong, bayonet-shaped spine situated behind the vent, and is an inch long."

Sim clearly had an *Aphanopus carbo,* at that time unrecognised in the British fauna but since found to be common along the 100 fathom line, where it may sometimes be taken even by the hundred by vessels trawling for hake.

I have a monograph in preparation covering the anatomy and biology of this species.

Genus ***BENTHODESMUS*** Goode & Bean

Benthodesmus Goode & Bean, 1882, *Proc. U.S. Nat. Mus.* **4** : 379.

Type species *Lepidopus elongatus* Clarke. Three species.

Goode & Bean erected this genus on the occasion of their describing a fish from Newfoundland which they believed to belong to Clarke's New Zealand species (the holotype of which they had not seen) and attributed characters to *Benthodesmus* additional or contrary to those in Clarke's description. In 1895 (*Oceanic Ichthyology* : 206) they erected a new species *B. atlanticus* on their Newfoundland specimen, leaving the situation that *Benthodesmus* was based on a species which they had not seen. Since the holotype of *L. elongatus* has been lost I propose to request the International Commission on Zoological Nomenclature to recognize *B. atlanticus* G. & B. as the type-species of *Benthodesmus,* which would at the same time provide a more convenient reference point and a more satisfactory indication of Goode & Bean's intentions. It is practically certain that the two nominal species will eventually be shown to be identical, but for the present I am retaining them both until New Zealand material shall be forthcoming. *B. atlanticus* is a junior synonym of *Aphanopus simonyi* Steindachner.

Synonyms

Lepidopus (*non* Gouan, 1770) } Numerous authors ; for references see under synonymies
Aphanopus (*non* Lowe, 1839) } of species.

It has been suggested to me that *Benthodesmus* should be split and a new genus erected on *B. tenuis* (Günther). I am strongly opposed to any such action, being of the opinion that *B. tenuis* is the close ancestor of *B. elongatus* and that it would be improper to obscure this close relation in the way proposed.

In the event of a new genus being recognized there is some possibility of the name *Scarcina* Rafinesque (1810) being already available, with *S. argyrea* preceding *B. tenuis*. *Scarcina* has always been regarded as a junior synonym of *Lepidopus* Gouan (1770) and for reasons outlined on p. 94 I prefer to leave it so for the present.

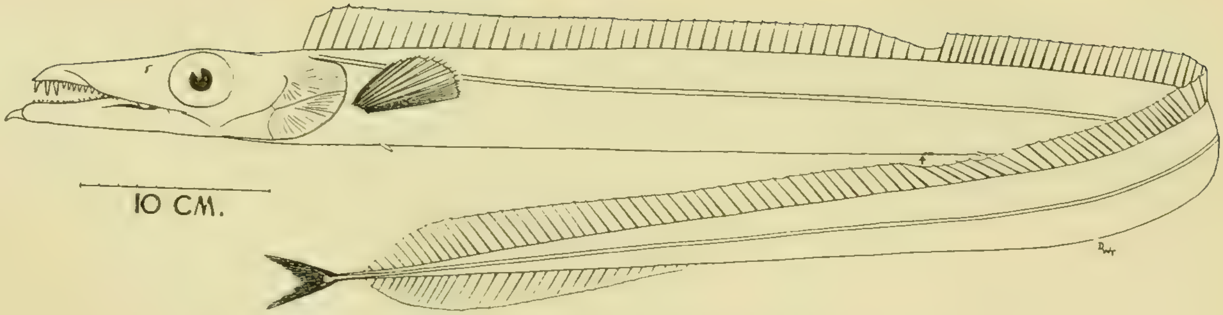

FIG. 8.—*Benthodesmus simonyi* (Steindachner). B.M. (N.H.) No. 1953.11.1.288. Madeira. 1,170 mm. S.L.

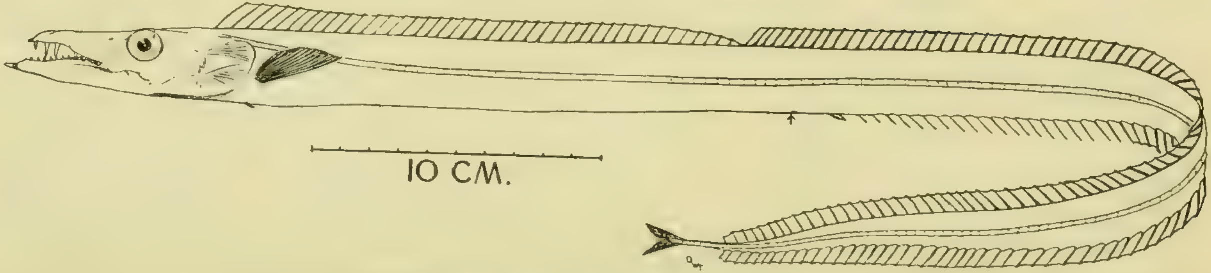

FIG. 9.—*Benthodesmus tenuis* (Günther). Holotype, 591 mm. S.L. (Fins much reconstructed from other specimens.)

DIAGNOSIS:

(1) Body very elongate; head-length 7·0–7·6 in standard length 221–591 mm., body-depth 23·8–34·4 in same (*B. tenuis*) *or* head-length 6·8–7·8 in S.L. 910–1225 mm., body-depth 21.7–27·0 (*B. simonyi*).

(2) Tail 55% (*B. tenuis*) or 60% (*B. simonyi*) of S.L.

(3) Vertebrae 47–52 + 75–80 = 123–131 (*B. tenuis*) *or* 52–53 + 101–103 = 153–156 (*B. simonyi*).

(4) Spinous dorsal base half as long as soft dorsal base.

(5) Dorsal spines 39–42, dorsal soft rays 80–88 (*B. tenuis*) *or* dorsal spines 45–46, dorsal soft rays 102–108 (*B. simonyi*).

(6) The number of soft dorsal rays is very close to that of the caudal vertebrae. There are very few intercalated interneural elements, which are usually toward the beginning or end of the fin.

(7) Anal spines i + I, the former extremely minute and completely concealed in the adult. I is a delicate cardiform scute with a median keel projecting as a short point between the two rounded posterior lobes.

(8) Anal spine i articulates a short distance in front of I. Their common basal element is a complex representing three or more fused elements. The interhaemal spine is a thin keel supported by three slender, tubular, cartilage-tipped spines (*B. tenuis*) or is completely wanting (*B. simonyi*). The horizontally-directed basal occupies the length of three vertebral centra.

(9) A complete external anal fin of 70–76 split but unbranched rays extending from the anal spines nearly to the caudal (*B. tenuis*) or with the anterior rays wanting and the external fin posterior and reduced to about 25 rays (*B. simonyi*).

(10) Ventral fins inserted immediately before perpendicular through anterior end of pectoral base (*B. tenuis*) or immediately behind perpendicular through posterior end of pectoral base (*B. simonyi*).

(11) Ventral fin I, 1 (soft ray always present ?); a scale-like spine and an internal rudimentary soft ray shorter than the scale.

(12) The principal teeth of the premaxillary and dentary series are without obvious barbs and without special enamel thickenings at the tips. When barbs are present, usually on the premaxillary fangs, they are barely perceptible and confined to the hinder edges. The margins of the teeth are smooth in both jaws.

(13) Palatine teeth present in a linear series, exposed (*B. tenuis*) or concealed under mucosa (*B. simonyi*).

(14) Principal teeth on first gill-arch few, teeth becoming progressively reduced on subsequent arches.

(15) Intermuscular bones (pleurals and epipleurals) reduced.

(16) Pigmentation uniform silver sprinkled black. Melanophores thinly distributed, except for denser aggregations along lateral line and along median dorsal and ventral lines. Dark spots at bases of dorsal and anal rays, preceded by large individual stellate melanophores in juveniles. Fins shaded with pastel colours.

Key to Species

Ventral fins inserted before anterior end of pectoral base.

Dorsal rays 120–133; anal elements i + I + 70–76 with external rays throughout; vertebrae 123–131; lateral line strongly developed (less than 15 times in height at pectoral)

Benthodesmus tenuis (Günther) E. Equatorial Atlantic; Gulf of Mexico; Indo-Pacific.

Ventral fins inserted behind posterior end of pectoral base.

Dorsal rays 147–155; anal elements i + I + 91–99 with external rays substantially confined to posterior third; vertebrae 153–158; lateral line less strongly developed (more than 20 times in height at pectoral)

Benthodesmus elongatus (Clarke) New Zealand; Australia; S. E. Africa (?)

Benthodesmus simonyi (Steindachner) N. Atlantic; N.E. Pacific

For full discussion and complete bibliographies see :—

Tucker, 1953, *Proc. zool. Soc. Lond.* **123** : 171–197, pls. and text-figs.

—— 1955, *Bull. Mus. Hist. nat. Belg.* **31**, No 64: 1-26, 1 pl. and text figs.

Benthodesmus elongatus (Clarke)

Lepidopus caudatus (*non* Euphrasen, 1788) Hutton, 1872, *Fishes of New Zealand* : 13.

Lepidopus elongatus Clarke, 1879, *Trans. N.Z. Inst.* **11** : 294, pl. 14.

Holotype should be in the Dominion Museum, Wellington, N.Z., but cannot be found (*fide* Mr. J. Moreland *in litt.*). Type locality Hokitika Beach, W. coast of South Island, New Zealand.

Benthodesmus elongatus (part), Goode & Bean, 1882, *Proc. U.S. Nat. Mus.* **4** : 380.

Lepidopus (*Benthodesmus*) *elongatus* McCulloch, 1915, *Biol Res. " Endeavour,"* **3** : 152.

? *Benthodesmus atlanticus* (*non* Goode & Bean, 1895) Gilchrist & Von Bonde, 1924, *Rep. Fish. Mar. biol. Surv. S. Afr.* **3**, Spec. Rep. 7 : 16.

? *Benthodesmus tenuis* (*non* Günther, 1877) J. L. B. Smith, 1949, *Sea Fishes S. Africa* : 312.

Benthodesmus simonyi (Steindachner)

(Text-fig. 8).

? *Lepidopus elongatus* Clarke, 1879, *Trans. N.Z. Inst.* **11** : 294, pl. 14. (See above.)

Benthodesmus elongatus (part), Goode & Bean, 1882, *Proc. U.S. Nat. Mus.* **4** : 381.

Aphanopus simonyi Steindachner, 1891, *S.B. Akad. Wiss. Wien* **100** : 356.

Holotype should be in the Naturhistorisches Museum, Vienna, but cannot be found (*fide* Dr. D. Kähsbauer, *in litt.*). Type locality N.E. from S. Cruz de Teneriffe, Canary Is.

Benthodesmus atlanticus (part) Goode & Bean, 1895, *Oceanic Ichthyology* : 206.

Holotype U.S. Nat. Mus. Washington No. 29116. Type locality W. edge Grand Bank of Newfoundland. (The two smaller specimens mentioned are *Diplospinus multistriatus* Maul, *fide* Dr. Carl L. Hubbs *in litt.*)

Lepidopus sp. Vieira, 1895, *Ann. Sci. nat. Pôrto* **1** : 165, upper figs. pl. 9 and 10.

Lepidopus atlanticus, Boulenger, 1899, *Ann. Mag. nat. Hist.* (7) **3** : 180.

Lepidopus (*Benthodesmus*) *atlanticus* Saemudsson, 1921, *Skýrsla um hide islenzka náttúrufraedisfjelag* **1919–20** : 37.

Benthodesmus tenuis (*non* Günther, 1877) (part) J. L. B. Smith, 1949, *Sea Fishes S. Africa* : 312. (Figure copy of *B. atlanticus* from G. & B. 1895.)

Benthodesmus simonyi Maul, 1953, *Proc. zool. Soc. Lond.* **123** : 167.

Benthodesmus tenuis (Günther)

(Text-fig. 9)

Lepidopus tenuis Günther, 1877, *Ann. Mag. nat. Hist.* (4) **20** : 437.
Lepidopus tenuis Günther, 1887, " *Challenger* " *Reps. Zool.* **22** : 37, pl. 7, fig. B.
Holotype B.M. (N.H.) No. 1879.5.14.297. Type locality " Challenger " St. 232, 35° 11′ 0″ N., 139° 28′ 0″ E., off Inosima, Sagami Bay, Japan.
Benthodesmus tenuis, Goode & Bean, 1895, *Oceanic Ichthyology* : 206.
Benthodesmus elongatus (*non* Clarke, 1879) *idem. loc. cit.* (figure only, a reversed tracing from Günther, 1887).
Lepidopus aomori Jordan & Snyder, 1901, *J. Coll. Sci. Tokyo,* **15** : 303.
Holotype in the Aomori Museum, Japan. Type locality Aomori Bay.
Benthodesmus benjamini (part) Fowler, 1938, *Proc. U.S. Nat. Mus.* **85** : 45, fig. 16.
Holotype U.S. Nat. Mus. No. 98821. Paratypes 98822–5. Type locality " Albatross " St. D.5445, off Philippine Is. (The paratype material is contaminated with *Diplospinus multistriatus* Maul, *fide* Dr. Carl L. Hubbs, *in litt.*)
Benthodesmus atlanticus (*non* Goode & Bean, 1895) Longley & Hildebrand, 1941, *Cat. Fish. Tortugas* : 73.
? *Lepidopus argenteus* (*non* Bonnaterre, 1788) Brauer, 1906, *Wiss Ergebd.* " *Valdivia,*" **15** : 292, taf. 12, fig. 3. (Fig. erroneously captioned *L. gracilis.*)

Benthodesmus sp. incertae sedis

Lepidopus tenuis (? *non* Günther, 1877) Franz, 1910, *Abh. Bayer. Akad.* **4** Suppl. Bd. **1** : 56. (Locality Uraga Channel, Japan.)

On the information available this specimen cannot be assigned with certainty to either *B. simonyi* or *B. tenuis*. I do not believe it to be a new species, nor do I accept Franz's opinion that it justifies regarding this genus as containing one world-wide species.

Subfamily LEPIDOPODINAE Gill

Lepidopodinae Gill, 1863, *Proc. Acad. nat. Sci. Philad.* **1863** : 227.

Type genus *Lepidopus* Gouan.

Genera now recognised.—*Lepidopus* Gouan ; *Evoxymetopon* (Poey) Gill ; *Eupleurogrammus* Gill ; *Assurger* Whitley ; *Tentoriceps* Whitley.

Diagnosis :

(*Note.*—Since there is considerable diversity among the genera of Lepidopodinae and since, through inadequate descriptions and lack of study-material, certain characters have not been verified in *Evoxymetopon*, *Assurger* and *Tentoriceps*, it is necessary to introduce qualifications into the following diagnosis. For this purpose the abbreviations *Lep.*, *Evox.*, *Eupl. Ass.*, & *Tent.* have been used for the generic names).

A. Slope of snout variable, gentle to steep ; orbits barely entering upper profile of head (*Lep.*) or more or less remote from it (all other genera) ; posterior confluence of frontal ridges elevated to support a sagittal crest at the nape which (in all genera except *Lep.*) is continued forward along the snout as a ridge-like elevation of the entire ethmofrontal region.

B. Cartilaginous protuberance at mandibular symphysis weak or absent ; a small, soft projection at the tip of the snout.
C. Lower hind margin of operculum markedly convex.
D. Teeth of main series without barbs. (*Lep.*, *Eupl.*, *Evox.*, *Tent. Ass.*). (Fangs slightly barbed in *Lep.*).
E. Teeth on palatines in a linear series. (*Lep.*, *Evox.*, *Eupl.*)
F. Lateral line descending gently from the shoulder and running in a median or sub-median postiion along the body, i.e. distance between lateral line and ventral profile at anus much more than half distance between lateral line and dorsal.
G. Spinous dorsal fin short, with 10 (*Evox.*), 9 (*Lep.*) or 3 (*Eupl.*) rays. Spinous and soft dorsals continuous, without any intervening notch.
H. Soft dorsal rays precisely corresponding to adjacent caudal vertebrae, each basal and interneural element being related to a neural spine. (*Lep.*, *Eupl.*)
I. Spinous anal i (*Lep.*, *Eupl.*) + I (all genera) ; anterior soft anal rays not penetrating skin (*Lep. Eupl. Evox. Ass.*) and external and functional fin effectively confined to posterior *ca.* 20 rays, or (in *Eupl.*) absent.
J. Terminations of dorsal and anal fins sub-opposite (*Lep.*, *Evox. Ass.*) or anal extending alightly beyond dorsal (*Eupl*).
K. Caudal fin present, small, normal, forked (*Lep.*, *Evox.*, *Ass.*) or absent (*Eupl.*, *Tent.*)
L. Ventral fins always present, composed each of a scale-like spine and sometimes at least (*Lep.*) an internal rudimentary soft ray ; insertion retarded, 1 to 5 eye-diameters behind posterior end of pectoral base.
M. Pyloric caeca *ca.* 24 (*Lep.*, *Eupl.*)

Osteological literature

Günther, 1860, *Cat. Fish. B.M.* **2** : 345–346 (short desc. *Lepidopus*).
Starks, 1911, *Stanford Univ. Publ.* **5** : 17–26, pl. (skull of *Lepidopus*).
Tucker, 1953, *Proc. zool. Soc. Lond.* **123** : 196, pls. (paired fins and anal of *Lepidopus*).

Literature on young stages

Delsman, 1927, *Treubia* **9**, Livr. 4 : 338 (*Eupleurogrammus* eggs and larvae).
Regan, 1916, *Sci. Rep. Brit. Antarct. Exped. Zool.* **1** : 144, pl. 8 (young *Lepidopus*).
Strubberg, 1918, *Rep. Dan. Oceanogr. Exped.* **2** Biol. A. 6. II : 7–16 (life-history of *Lepidopus*).

Genus ***LEPIDOPUS*** Gouan

Lepidopus Gouan, 1770, *Hist. Piscium* : 107, 185, Tab. 1, fig. 4.

No type species designated. Two species.

The earliest available binomen is *L. argenteus* Bonnaterre, 1788, *Encycl. Méth. Zool. Icht.* : 58, pl. 87, fig. 364. Bonnaterre's figure is an accurate reversed tracing of Gouan's caricature, but *L. argenteus* is a synonym, and almost certainly a junior synonym, of *Trichiurus caudatus* Euphrasen, 1788, *Handl. K. Vetensk. Akad. Stockholm* **9** : 52, tab. 9, fig. 2.

Euphrasen's paper appears in the section of the *Handl. K. Vetensk. Akad.* for Jan., Feb., Mar., 1788, the sections having been issued quarterly with separate title-pages though paginated in annual volumes.

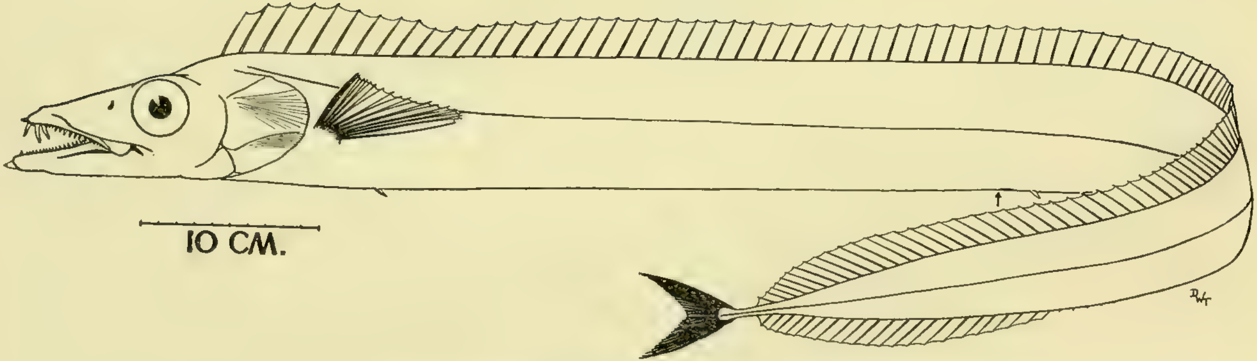

FIG. 10.—*Lepidopus caudatus* (Euphrasen). B.M. (N.H.) No. 1860.4.22.69.
Lisbon. 1,145 mm. S.L.

In their third and final attempt to establish the dates of publication of the parts of the *Encyclopédie Méthodique*, Sherborn & Woodward, 1906, *Ann. Mag. nat. Hist.* (7) **17** : 578 could establish nothing more precise concerning Bonnaterre's *Ichtyologie* than that it appeared in livraison 28 of the *Encyclopédie* issued sometime in 1788. Since, however, the livraisons were issued in order and the date April, 1788, can be assigned to livraison 26 the balance of probability favours Euphrasen's publication as the earlier one. Following the nomenclatorial orgy at the earlier part of the nineteenth century Euphrasen's name has been the more generally used.

Synonyms

(The full references to the following are given in the synonymy of *Lepidopus caudatus*, p. 93).

Trichiurus (*non* Linnaeus, 1758) Vandelli, 1797 ; Holten, 1802.
Vandellius Shaw, 1803. Type species *Vandellius lusitanicus* Shaw (*ex* Vandelli MS.).
Ziphotheca Montagu, 1809. Type species *Ziphotheca tetradens* Montagu.
Xiphotheca }
Xipotheca } variant spellings by later authors.
(NON *Zyphotheca* Swainson, 1839.)
? *Scarcina* Rafinesque, 1810. Type species *Scarcina argyrea* Rafinesque.

DIAGNOSIS (based on *L. caudatus*) :

(1) Body elongate, head 5·8–7·1 in standard length, greatest depth 10·8–18·3 in standard length (57–1224 mm.)
(2) Upper profile of head oblique-concave, rising at about 25° to the longitudinal axis from above the snout tip to behind the orbits and thereafter more steeply to the dorsal origin ; straight before the orbits. Ethmo-frontal region not elevated, posterior confluence of frontal crests strongly elevated. Interorbital slightly concave with very low longitudinal ridges.
(3) Orbit large, 4·9–5·6 in head, touching dorsal profile.
(4) Dorsal IX, 90–96 ; aggregate 99–105. The first dorsal spine is not enlarged, save as a transient larval character.
(5) Anal spines i + I ; I is a small triangular scale 2 or more in the pupil.
(6) Anal fin elements i + I + 61–64 ; anterior rays reduced or absent, posterior 20–24 rays supporting fin.
(7) Posterior end of operculum a broadly rounded point, barely reaching to anterior end of pectoral base.
(8) Ventral fins present, scale-like, inserted an eye-diameter behind the posterior end of the pectoral base.
(9) Caudal fin present.
(10) Vertebrae 41 + 70–73 = 111–113.

Key to Species

Dorsal rays 99–105 ; external anal fin reaching only half way to vent. D.IX, 90–96 ; anal elements i + I + 61–64 (the last 20–24 only being external fin-supporting rays) ; vertebrae 41 + 70–73.

Head 5·8–7·1 in standard length 57–1224 mm. ; depth 14·4 (–18·3)–10·8 in same ; eye 4·9–5·6 in head.

Ventral fins I-1 (1 is an internal rudiment only 1 mm. long in the adult fish), inserted an eye-diameter behind the pectoral base ; anal spine I is a small triangular scale, less that the pupil. Pyloric caeca 20 +. Colour uniform silvery.

Lepidopus caudatus (Euphrasen).
Atlantic, Mediterranean, S. Indian Ocean, S. Pacific.

Dorsal rays 82–87 ; external anal fin reaching to vent.

Analysis of dorsal spines and rays not known ; external anal i + I + 45–58 ; vertebrae unknown.

For body proportions see discussion.

Ventral fins I–1 inserted on or immediately behind perpendicular through posterior end of pectoral base ; anal spine I is long, keeled, about three-quarters the diameter of the eye. Pyloric caeca unknown.

This compromise description, based on Jordan & Evermann (1898) and Brauer (1906), may include two species or one, of uncertain systematic position, and without valid name(s). The discussion on pp. 95–7 explains this unhappy situation.

" *Lepidopus Xantusi* " Goode & Bean
California, Gulf of Guinea.

Lepidopus caudatus (Euphrasen)

(Text-fig. 10).

Trichiurus caudatus Euphrasen, 1788, *Handl. K. Vetensk. Akad. Stockholm,* **9** : 52, tab. 9, fig. 2.
Holotype in Alströmerika Museum ? Type locality Cape of Good Hope.
Lepidopus caudatus, White, 1851, *List Brit. Anim. B.M.* **8** Fish : 32.
Lepidopus argenteus Bonnaterre, 1788, *Encycl. Méth. Zool. Ichth.* : 58, pl. 87, fig. 364.
(*Ex* Gouan, 1770.) (See note under *Lepidopus* p. 90.) There is a partial confusion with *Lepturus argenteus* Linnaeus, 1754 (= *Trichiurus*) in the text.
Trichiurus ensiformis Vandelli, 1797, *Mém. Acad. Sci. Lisboa,* **1** : 70 (*nomen nudum*).
(*id. fide* Nobre, 1935, *Faun. Mar. Portugal,* **1** Vert. : 260).
Lepidopus ensiformis, Swainson, 1839, *Lard. Cab. Cycl. Fish.* **2** : 254.
Lepidopus gouanianus Lacépède, 1800, *Hist. nat. Poissons* **2** : 519.
(*Ex Gouan,* 1770.)
Lepidopus gouani Bloch & Schneider, 1801, *Syst. Ichth.* **1** : 239, tab. 53, lower fig.
(*Ex* Gouan, 1770.)
Trichiurus gladius Holten, 1802, *Skr. nat.-Selsk. Kbh.* **5**, Heft 2 : 23, Tab. 2, fig. 1.
Holotype in Copenhagen Museum ? Type locality Portugal. (I am doubtful whether this name should not perhaps be attributed to Abildgaard.)
Vandellius lusitanicus Shaw, 1803, *Gen. Zool. Pisc.* **4** (2) : 199.
(*Ex* Vandelli MS.)
Lepidopus lusitanicus, Leach, 1815, *Zool. Misc.* **2** : 7, pl. 62.
Ziphotheca tetradens Montagu, 1809, *Mem. Werner. N. H. Soc.* **1** : 81.
Holotype B.M. (N.H.) No. 1955.6.2.1. Type locality English Coast.
Lepidopus tetradens, Fleming, 1828, *Hist. Brit. Anim.* : 205.
Lepidopus peronii Risso, 1810, *Ichth. Nice* : 148, Pl. 5, fig. 18.
Type locality Nice.
? *Scarcina argyrea* Rafinesque, 1810, *Car. n. gen.* : 20, pl. 7, fig. 1.
Type locality Sicily.
? *Lepidopus argyreus*, Cuvier, 1829, *Règne Animal* 2 Ed. **2** : 217.
Lepidopus govanianus Risso, 1826, *Hist. Nat.* **3** : 290.
(*Ex* Gouan, 1770.)
Lepidopus lex Phillips, 1932, *N.Z. Journ. Tech.* **13** : 232.
Syntypes in Dominion Museum, Wellington ? Type locality New Zealand. (*Lepidopus caudatus* of other New Zealand authors ; *non L. caudatus* Hutton, 1872, *Fishes N.Z.* : 13, who had *Benthodesmus elongatus* (Clarke).)
Aphanopus carbo (non Lowe, 1839) (part) Norman, 1937, in Fraser and Norman, Giant Fishes, Whales and Dolphins : 140.
non Lepidopus caudatus Sim, 1898, *Ann. Scot. nat. Hist.* **1898** : 53 (mis-identification of *Aphanopus carbo* Lowe).
non Lepidopus elongatus Clarke (1879) ; McCulloch (1915) (see *Benthodesmus elongatus*).

non Lepidopus sp. Vieira (1895).
non Lepidopus atlanticus, Boulenger (1899) ; Saemundsson (1921) } (See *B. simonyi*.)
non Lepidopus aomori Jordan & Snyder (1901)
non Lepidopus argenteus Brauer (1906) } (See *Benthodesmus tenuis*.)

The nineteenth century synonyms listed above have been pretty generally accepted; I have verified each of them, so far as the accompanying data allow, and do not propose to attempt any individual justifications in the present short summary. Only *Scarcina argyrea* Rafinesque (1810) calls for any urgent comment. This name has been copied as a synonym of *Lepidopus caudatus* by many authors, but the figure shows a head and body-form very reminiscent of a *Benthodesmus* and the stated dorsal count (125) falls within the range of *B. tenuis* (Günther) and is well above the D.99–105 found in *L. caudatus*. The anal count of 15 and the anal fin as figured are, however, quite like *Lepidopus*. Since *Benthodesmus* is not yet known from the Mediterranean it is better to regard Rafinesque's as an inaccurate impression of *L. caudatus* for the present. Should *B. tenuis* be found in the Mediterranean *Scarcina argyrea* will have to be considered as a senior synonym and it may be thought desirable to invoke the Plenary Powers of the International Commission in order to suppress it. *Scarcina* would also precede *Benthodesmus*.

Norman (1937) mentions *Aphanopus carbo* as being " not uncommon in the fish markets of the Mediterranean ". In an intensive study of *A. carbo* I have so far found nothing to confirm this statement, which may have been made through some confusion of vernacular names. Thus the Portuguese and Madeiran fishermen call *A. carbo* " O Peixe Espada preta " and *L. caudatus* " O Peixe Espada branca " (Black and White Scabbard-fishes, respectively), and in both cases " Peixe-espada " or " Espada" for short.

Phillipps (1932) :

> " examined several frost-fish and found consistent, though slight, differences between the New Zealand and Atlantic species . . . 3 to 4 less rays in the dorsal fin, 3 or 4 less anal rays, and a total length of head under 7 in total length. Goode and Bean's figure shows a species with a longer head, and no dorsal spines of greater length than the diameter of the eye. In the New Zealand fish the height of the sixth dorsal ray is 5 in the head while in the European fish the height of this ray is about 8 or more in the head. The tail of the New Zealand frost-fish is not so deeply emarginate and agrees more nearly with that of *Evoxymetopon taeniatus* figured by Goode and Bean."

Phillipps is presumably referring to Goode & Bean (1895) *Oceanic Ichthyology*, Plate 58, figs. 213 and 214. I have dealt in some detail with the identification of fig. 213 under "*Lepidopus Xantusi*" (p. 96 *q.v.*) and so for the present it is sufficient to state that this figure is a poorish figure of an apparent young *Lepidopus caudatus* and not a very satisfactory basis for any comparison. The head in Goode & Bean's figure goes about 7·5 in the total length and is therefore shorter, not longer as stated by Phillipps, and typical of a juvenile as opposed both to post-larval and adult specimens. The dorsal spines and tail of Goode & Bean's figure are useless as evidence.

Comparing specimens of as nearly equivalent size as possible I obtain the following results:

TABLE II.

	Lepidopus caudatus.	
	Lisbon. No. 1860.4.22.69.	New Zealand. No. 1903.4.30.29.
Standard length	1142 mm.	1224 mm.
Head in S.L.	7·13	6·65
Depth in S.L.	15·43	10·83
Eye in head length	4·92	5·41
6th dorsal spine in H.L.	5·33	5·25
Dorsal count	D.IX, 96	D.IX, 90
Anal count	A.i+I+40+24	A.i+I+41+20

Apart from the greater depth of the body, in part attributable to age, the New Zealand specimen appears to show only the trivial differences to be expected in material of a widely ranging pelagic fish taken from the extreme limits of its distribution. The variations are no greater than those found in Trichiurid species, of which I have been able to study substantial samples and accordingly I am not at present prepared to accept *Lepidopus lex* Phillipps as distinct from *L. caudatus* (Euphrasen).

If, however, the separation of *L. lex* should be considered justified an interesting situation arises. Since the type locality of *L. caudatus* is the Cape of Good Hope it is likely that the antipodal forms will be conspecific but distinct from those of the E. Atlantic and Mediterranean. *L. lex* would therefore still fall as a synonym of *L. caudatus*, but *L. argenteus* Bonnaterre (1788) would have to be revived. A further complication would arise in that the *Lepidopus caudatus* figured by Goode & Bean (1895) and uncertainly associated with the holotype of *L. xantusi* G. & B. appears to have the lower dorsal count of *L. lex* also. (Further discussion under *L. xantusi*, p. 96).

"Lepidopus xantusi" Goode & Bean

Lepidopus caudatus (? *non* Euphrasen) Jordan & Gilbert, 1882, *Proc. U.S. Nat. Mus.* **5** : 358.
Lepidopus caudatus (? *non* Euphrasen) (part) Goode & Bean, 1895, *Oceanic Ichth.* : 203, (?) fig. 213.
Lepidopus caudatus (? *non* Euphrasen) Jordan & Evermann, 1896, *Bull. U.S. Nat. Mus.* No. **47** : 886.
Lepidopus caudatus (? *non* Euphrasen) Jordan & Evermann, 1900, *Bull. U.S. Nat. Mus.* No. **47**, (?) pl. 136, fig. 373.
Lepidopus xantusi Goode & Bean, 1895, *Oceanic Ichth.* : 519.
Holotype U.S. Nat. Mus. No. 10115. Type locality Cape San Lucas, California.
Lepidopus xantusi Jordan & Evermann, 1898, *Bull. U.S. Nat. Mus.* No. **47** : 2843.
Lepidopus xantusi Jordan & McGregor, 1899, *Rep. U.S. Fish. Comm.* **24** (1898) : 276.
Lepidopus xantusi ? Brauer, 1906, *Wiss. Ergebd. " Valdivia,"* **15** : 291, taf. 12, fig. 2.

The circumstances surrounding the publication of this species are so wretchedly unsatisfactory that a new name will have to be found for it by the first worker able to re-describe it from material.

Jordan & Gilbert (1882) list U.S. Nat. Mus. No. 10115, " One specimen, 10 inches long, in poor condition " as " *Lepidopus caudatus* (Euphr.) White " in a catalogue of the fishes collected by one John Xantus at Cape San Lucas, California. (The reader should beware confusion with the Joanne Xantus whose Asian collections were published by Karoli.)

Goode & Bean (1895 : 203) give a description of *L. caudatus* evidently taken from Günther whose name is, in fact, cited. They then refer to a Xantus specimen and on p. 13 of the accompanying *Atlas* of plates they state that their figure of *L. caudatus* is drawn from U.S. Nat. Mus. No. 10115, collected by John Xantus, off Cape St. Lucas. On p. 519 of an appendix to the main text, however, this specimen becomes the type of a new species with the brief remark :

> " The specific identity of the fish found at St. Lucas by Xantus is so doubtful that we prefer to refer to it as *L. Xantusi*, new specific name."

We are left to consider whether Article 21 of the *International Rules* has been complied with ; on the text alone *L. Xantusi* is a *nomen nudum* and may be saved only by the figure, to be discussed presently.

Jordan & Evermann (1896) give the Günther-Goode & Bean version of *L. caudatus* (with an addition of pure Günther) and conclude by assigning the Xantus specimen once again to *L. caudatus*. Jordan & Evermann (1898) have realized that *L. Xantusi* exists and that somebody should give a description of it, but instead of describing it from the holotype (10 inches S.L.) they elect to do so from a second Cape San Lucas specimen which is more portable (5½ inches S.L.). Jordan & Evermann (1900), however, continue to publish Goode & Bean's original figure of the supposed holotype of *L. Xantusi* still with the legend " *L. caudatus* ".

The figure published by Goode & Bean has no scale of magnification nor do these authors anywhere state the size of their specimen ; for that we have to return to Jordan & Gilbert (1882). Moreover the drawing has the tail nicely curved, an effective obstruction to accurate measurement of standard length. I derive the following data :

Radial Formula D.99 ; A. (external) 18.

		(mm.)
	Measured distance from snout tip to D.30	125
	Estimated distance from D.30 to D.70 (taken as 4 × mean distance) D.20–30 and D.70–80)	120
	Measured distance from D.70 to tip caudal peduncle	79
Whence	Estimated standard length of figure	324

Head in S.L. 7·3 ; depth in S.L. 18·6 ; eye in head 5·7 ; snout in head 3·1
Insertion of ventral fins an eye-diameter behind pectoral base.

But these are the counts found in *Lepidopus caudatus* (Euphrasen) and these the body-proportions of a young fish of that species ! We are therefore driven to one of two conclusions :

Either (1) The figure is drawn, by some accident, from a specimen other than the holotype of *L. Xantusi* Goode & Bean. In this case the name *L. xantusi* Goode & Bean falls as a synonym of *L. caudatus* (Euphrasen) ; whatever the identity of the *Xantus specimen*, no "definition or description" have been published, nor any figure *of that specimen*. Further, although Jordan & Evermann (1898) and Brauer (1906) give adequate characterisations of a species distinct from *L. caudatus* (Euphrasen) under the name *L. Xantusi*, their name must fall as a homonym of *L. Xantusi* Goode & Bean under Article 35 of the *Rules*.

or (2) The figure is drawn from U.S. Nat. Mus. No. 10115 as stated and represents the holotype of *L. Xantusi* G. & B. In this case *L. Xantusi* again falls as a synonym of *L. caudatus* (Euphrasen) and *L. Xantusi* Jordan & Evermann and *L. Xantusi* Brauer again fall, as homonyms, under Article 35 of the *Rules*.

The description by Jordan & Evermann (1898) is repeated *verbatim* by Jordan & McGregor (1899). I give the complete text :

> "Head 4 2/3 in body ; depth 3 in head ; eye 5 1/3 ; interorbital space 8 1/3 ; snout 3 ; maxillary 3 1/3. D.82 ; A.II, 45. Jaws with long, sharp teeth in front, followed by single rows of weaker ones, arranged in groups of twos and threes. Height of dorsal, near middle of body, 3 in head. Anal preceded by 2 scutes, the first minute, the second wide, strongly keeled, its length 3/4 the diameter of eye. Pectorals of 12 rays, length 2 in head. Each ventral consists of a flat keeled spine followed by a minute ray. This species is known from 2 small mutilated specimens, both found on the beach near San Jose del Cabo, Cape San Lucas. The type was taken by John Xantus, about 1860, and recorded by Jordan & Gilbert as *Lepidopus caudatus*. The second, of about the same size (5½ inches), was taken by Richard C. McGregor, in 1897. From the latter the above account was taken. The species differs from *Lepidopus caudatus* in the much shorter dorsal and longer anal. D.103 ; A. 24. (Named for John Xantus de Vesey)."

Additional data, not provided above, are now needed to decide whether this fish may remain in *Lepidopus* when a new name shall be assigned to it ; at present it could as well belong to an *Aphanopodine* genus as to *Lepidopus* and may even represent a new genus connecting *Diplospinus* and *Lepidopus*.

Brauer (1906) gives a description and figure of "*L. Xantusi*" from the Gulf of Guinea and discusses the difficulties of his identification in face of the above description. The size is not given, but since a scale of magnification is given for some of the other figures on the same plate (though not for this) we may assume X1, hence 151 mm. S.L. Brauer gives D.87 ; A.58 ; head 5·5 in S.L.; depth 15 in S.L. ; eye 5½ in head. It would help if Jordan & Evermann meant "Head 4 2/3 in body (less head)", i.e. 5 2/3 in S.L., which would also give depth 17 in S.L. instead of 14. The discrepancies between the fin-ray counts are obvious. The figure shows a head about intermediate in form between *Aphanopus* and *Lepidopus* and ventrals inserted barely behind the pectorals, not quite so far retarded as in *L. caudatus*. Clearly we should know more about these specimens.

Genus ***EVOXYMETOPON*** (Poey) Gill.

Evoxymetopon Poey, in Gill, 1863, *Proc. Acad. nat. Sci. Philad.* **1863** : 227.

Type species *Evoxymetopon taeniatus* (Poey) Gill. Monotypic, or two species.

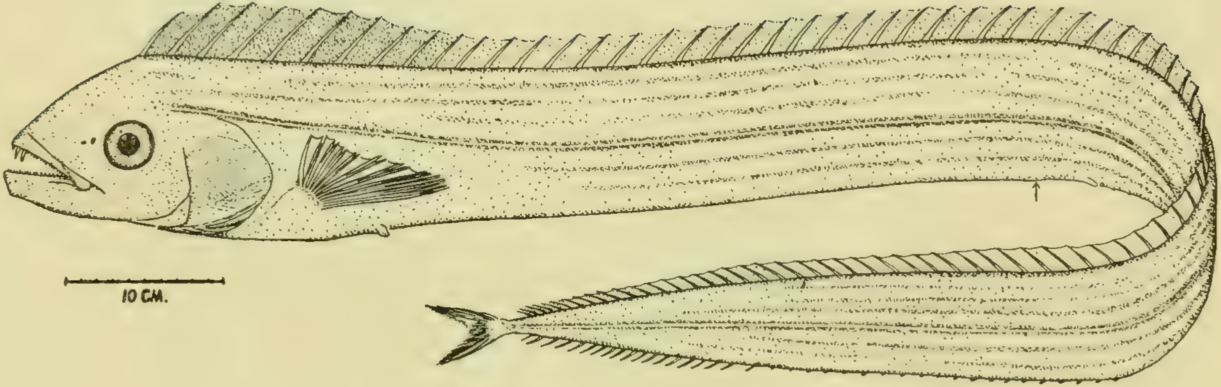

FIG. 11.—*Evoxymetopon taeniatus* (Poey) Gill. Holotype, 1,410 mm. T.L.
(Re-drawn, from Goode & Bean : scale added.)

DIAGNOSIS:

(1) Body elongate, head 8 in total length, greatest depth 12–13 in total length. (1410–1980 mm.)

(2) Upper profile of head convex, a steep continuous curve from the tip of the snout to the origin of the dorsal set at about 45° to the longitudinal axis; slightly convex before the orbits. Structure of cranial crest unknown, but evidently the ethmo-frontal region and the posterior confluence of the frontal crests are both elevated. Interorbital strongly convex.

(3) Orbit large, 5–6 in head length, an eye-diameter ± below the dorsal profile.

(4) Dorsal X, 77; aggregate 87. The first dorsal spine may be enlarged, nearly as long as the head.

(5) Anal spines i(?) + I; I is a keeled scale.

(6) Analysis of anal fin elements unknown; the anterior rays, if present, appear barely to penetrate the skin while the posterior *ca.* 20 only are fin-supporting rays.

(7) Posterior end of operculum a broadly rounded point falling less than a pectoral base short of the pectoral base.

(8) Ventral fins present, scale-like, inserted an eye-diameter behind the posterior end of the pectoral base.

(9) Caudal fin present.

(10) Analysis of vertebrae unknown.

Evoxymetopon taeniatus (Poey) Gill

(Text-figs. 11 12 13)

Evoxymetopon taeniatus Poey, in Gill, 1863, *Proc. Acad. nat. Sci. Philad.* **1863**: 228.
Holotype U.S. Nat. Mus. No. 5735. Type locality Havana, Cuba.
Evoxymetopon taeniatus Poey, 1873, *Ann. Soc. Esp. Hist. nat. Madrid,* **2**: 77, pl. 5.
Evoxymetopon taeniatus Goode & Bean, 1895, *Oceanic Ichthyology*: 204, fig. 214.
? *Evoxymetopon poeyi* Günther, 1887, "*Challenger*" *Reps. Zool.* **22**: 39, pl. 43.
Disposal of holotype unknown. Type locality Mauritius.
(For *Evoxymetopon anzac* Alexander see under *Assurger,* p. 106.)

It is curious that Poey should have waited ten years before publishing his own description and first figure of this species. Goode & Bean give a new figure of the holotype but their description appears to be derived entirely from Gill and their only original contribution is to confuse Gill's percentages with millimetres and so to mislead others into believing that the specimen is only one-fourteenth of its true length.

Evoxymetopon poeyi, described "with great hesitation . . . as a second species" was based on a dry skin which Günther received from Mauritius while his "Challenger' Report was passing through the press. The ownership and ultimate destination of this specimen are unstated and unknown; there is certainly no evidence that it ever became part of the permanent collections of the British Museum (Natural History).

The salient characters of these two fishes, as compiled from the literature, are given in Table III, from which it is apparent that there is a large measure of agreement between them and that the differences are readily attributable to age or sex, damage or misinterpretation.

The elongated first dorsal spine noted in *E. poeyi* is a striking feature and apparently unique among adult Trichiurids; though it occurs in the young stages of *Lepidopus* it does so only as a transitory condition and one to be regarded, like the disproportionate ventral fins, as a flotation device, parallelled among many other young Teleosts and without phyletic significance. *E. taeniatus* and *E. poeyi* may be female and male of one species (c.f. *Anthias*) or there may be growth changes between 1410 and 1981 mm. length, but a quite likely explanation is that the Cuban specimen may be damaged.

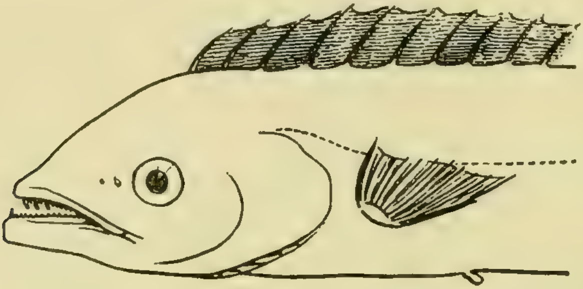

FIG. 12.—*Evoxymetopon taeniatus* (Poey) Gill. Head of holotype, 1,410 mm. T.L. (from Poey).

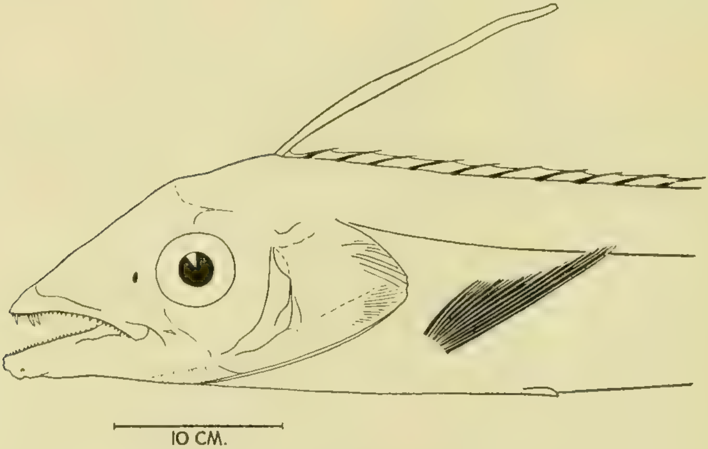

FIG. 13.—*Evoxymetopon poeyi* Günther. Head of holotype, 1,980 mm. S.L. (re-drawn, after Günther; scale added).

The homologies of the parts in other Trichiuridae studied indicate that the post-anal structures probably comprise the usual minute spinule (so far overlooked) and a broad scale having a median depression or keel, the pair articulating with a simple or compound basal structure. Experience with damaged *Benthodesmus* material provides a ready explanation of how the discrepancies between the accounts of Gill, Poey and Günther may have arisen.

TABLE III.

	Evoxymetopon taeniatus (Poey) Gill.	*Evoxymetopon poeyi* Günther.
Total length	1410 mm. (Poey)	78 inches (Günther) (ca. 1981 mm.)
Greatest height/T.L.	1/12 (Gill)	1/13 or less (Günther)
Head length/T.L.	1/8 (Gill)	1/8 (Günther)
Orbit/head	1/6 (Gill)	1/5 (Günther)
Dorsal rays	X, 77 (D.87. "The first ten dorsal spines are undivided ; the rest split."—Gill.)	D.93 (Günther)
First dorsal spine	No special mention in either Gill or Poey.	" . . . large, compressed, sword-shaped . . . not much shorter than the head . . . loosely articulated with the interneural " (Günther).
Anal rays	A.19. "Anal spines numerous . . . mostly minute, free, posteriorly enlarged, connected by the membrane and forming a fin " (Gill). Upwards of 30 small spines figured anterior to the fin proper (Goode & Bean).	x + 20 (Günther) " . . . anal fin, the rays of which begin to be free in the posterior third of its extent " (Günther).
Post-anal scute	" Dagger-shaped spine behind the anus " (Gill). " A corta distancia posterior del ano la pequeña escama triangular y movediza senelada por Cuvier en el Lepidopo" (Poey).	(Gill's spine) " is entirely covered by skin, and consists of coalesced and flattened interhaemal elements . . . a single oval scale slightly bent along the middle occupies the space at a short distance behind the vent " (Günther).
Ventral insertions	About 1½ times the head length from the tip of the snout (17½ : 12—Gill).	About 1⅓ times the head length from the tip of the snout (313 : 240—Günther's fig.).
Vent	" Submedian " (Gill).	" Somewhat in advance of the middle of the total length " (Günther).
Coloration	" Silvery, with about six narrow reddish bands most distinct behind, the first on the ridge of the back and the fifth along the lateral line " (Gill).	" Uniform silvery " (Günther).

The upper profile of the head in *E. pocyi* does not rise quite as steeply as in *E. taeniatus* (a condition apparently related to allometric growth of the jaws) and the whole head is less plump in appearance. Here, again, one recalls post-mortem changes witnessed in freshly caught *Aphanopus carbo* off Madeira, as well as the fact that *E. pocyi* is figured from a dry skin, and accordingly one discounts the differences.

Gill (1863) alludes to a Scottish specimen referred by Hoy to *Trichiurus lepturus* (there were actually two) and suggests that it may have been an *Evoxymetopon. Evoxymetopon* has never been taken in British waters and Hoy's specimens must be referred probably to *Trachypterus* or *Regalecus*.

Although the osteology of *Evoxymetopon* is unknown it is certain that the ethmofrontal region of the skull, together with the posterior confluence of the frontal ridges must be elevated in much the same way as in *Eupleurogrammus*, but to a greater extent. This character apart *Evoxymetopon* stands fairly close to *Lepidopus* and is very near to the ancestor of *Eupleurogrammus*.

Genus ***EUPLEUROGRAMMUS*** Gill

Eupleurogrammus Gill, 1863, *Proc. Acad. nat. Sci. Philad.* **1863** : 226.
Type-species *Trichiurus muticus* Gray. Two species.
Trichiurus (part). Many authors, from Linnaeus (1758), whose type material of *Trichiurus lepturus* was contaminated with this genus. (See note under *Trichiurus*, p. 114).
Enchelyopus (part) Bleeker, 1872, *Ned. Tijdschr. Dierk.* **4** (1872) : 131.

DIAGNOSIS :

(1) Body very elongate, head 9·4–11·2 in total length, greatest depth (in region of vent) 14·7–17·6 in total length (273–617 mm.)

(2) Upper profile of head oblique to very slightly concave, rising from the tip of the snout in a line set at about 30° to the longitudinal axis and quite straight before the orbits. Cranial crest formed by elevation of ethmofrontal region and of the posterior confluence of the frontal crests. Interorbital strongly convex.

(3) Orbit small, 6·0–7·8 in head, ½ to ¼ an eye-diameter below the dorsal profile.

(4) Dorsal III, 123–131 or III, 143–147 ; aggregate 126–150. First dorsal spine not enlarged.

(5) Anal spines i + I ; I is a small triangular scale.

(6) Anal fin elements i + I + 114–121 ; the external fin is entirely suppressed and the ventral profile smooth.

(7) Posterior end of operculum a rounded point, overlying middle of pectoral fin and base.

(8) Ventral fins present, scale-like, inserted about 5 eye-diameters behind the posterior end of the pectoral base.

(9) Caudal fin absent.

(10) Vertebrae 32–35 + 125–128 = 157–162 or 41 + 150–151 = 191–192.

Key to Species.

Anal origin below D.33–37
D.III, 123–131 ; Vertebrae 32–35 + 125–128 = 157–162
Eupleurogrammus intermedius (Gray)
Indo-Pacific.

Anal origin below D.41–42
D.III, 143–147 ; Vertebrae 41 + 150–151 = 191–192
Eupleurogrammus muticus (Gray)
Indo-Pacific.

Eupleurogrammus intermedius (Gray)

(Text-fig. 14)

Trichiurus intermedius Gray, 1831, *Zoo. Misc.* **1** : 10.
Syn-types (3) B.M. (N.H.) No. 1869.3.19.76. Type locality Chusan.

Trichiurus muticus (*non* Gray) numerous authors. (Incorrect deductions from Gray's original description or from following Günther, 1860, *Cat. Fish. B.M.* **2** : 348 ; no new material involved.)

Trichiurus medius Griffith, 1834, Cuvier's *Anim. Kingd.* Pisces : 349 (*nom. emend.* from Gray).

Trichiurus savala (*non* Cuvier, 1829) (part) Bleeker, 1852, *Verh. Bat. Gen.* **24** Makr. : 41. (Determination altered to *T. glossodon* by Bleeker, see below.)

Trichiurus glossodon Bleeker, 1860, *Acta. Soc. Indo-Neerl.* **8.** Dertiende Bijdr. Visch. Borneo : 38.
? Syn-types, in Leiden Museum and in British Museum (Natural History), B.M. (N.H.) No. 1880.4.21.119. Type localities Java, Sumatra, Singapore, Bintang, Borneo.

Trichiurus glossodon De Beaufort, 1951, *Fish. Indo-Austr. Archip.* **9** : 190. (Bleeker's material re-examined.)

Trichiurus glossodon Delsman, 1927, *Treubia* **9,** livr. 4 : 338.

Günther (1860) regarded *Trichiurus intermedius* Gray as a synonym of *T. muticus* Gray. This error of judgment not only led almost every subsequent worker astray ; it also had the practical result that Gray's types in the British Museum (Natural History) were not properly recognized and segregated. There is, however, one jar, Reg. No. 1860.19.76, containing three specimens and bearing (among others) a label in an old hand stating :

> " *Trichiurus intermedius*
> Chusan. E. I. Company."

A second label, written in ink on paint, changes the identification to *Trichiurus muticus* and a third, overlying both, adds the Register number and changes the source to " Dr. Cantor's Colln." It is not possible to reconcile this material with any entry in Günther (1860), but there seems no doubt that these are the syntypes of *T. intermedius* Gray, both from their apparent history and their study.

Accordingly *T. intermedius* provides one of the major nomenclatorial surprises of the present paper. Even as a synonym of *T. muticus* it would, of course, have passed over into *Eupleurogrammus*, but, as shown in the key and in Table IV. *T. intermedius* proves to be a perfectly valid species. Further, on the evidence of a probable syntype of *T. glossodon* Bleeker and on De Beaufort's (1951) re-description of other presumed type-material of *T. glossodon* at Leiden, it becomes apparent that the more widely-recognized *T. glossodon* is only a synonym of *T. intermedius*, as

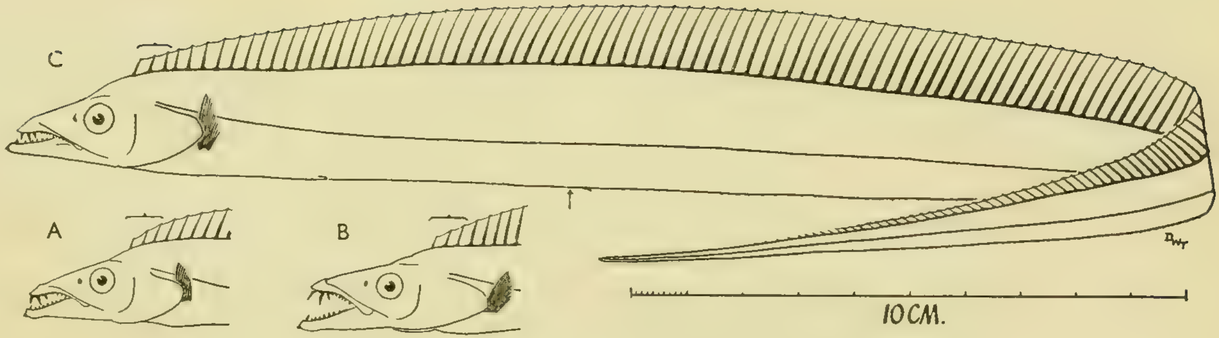

FIG. 14.—*Eupleurogrammus intermedius* (Gray). Syntypes. A., B., heads of specimens of 273, 308 mm. S.L., C., specimen of 336 mm. S.L.

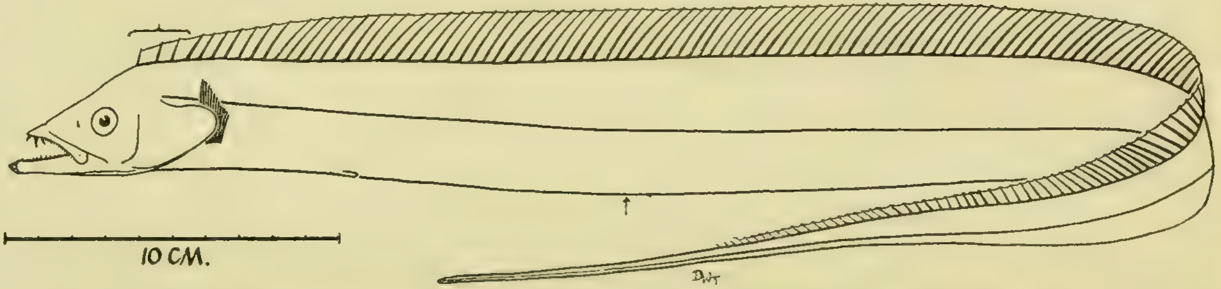

FIG. 15.—*Eupleurogrammus muticus* (Gray). Specimen of 617 mm. S.L. (*not* the holotype). No locality data.

TABLE IV.

	Standard Length (mm.).	Head in S.L.	Depth in S.L.	Eye in head.	Fin-ray counts :		A. origin below D.	Vertebral counts.
					D.	A.		
Eupleurogrammus intermedius :								
Trichiurus intermedius Gray								
Syn-types : Chusan : East India Co. Reg. No. B.M. (N.H.) 1860.3.19.76	273	10·11	17·61	6·00	III, 130	i+I+120	35–6	34+128=162
	308	9·77	17·11	6·56	III, 128	i+I+116	37	35+127=162
	336	10·29	16·39	6·56	III, 131	i+I+114	35	32+127=159
Trichiurus glossodon Bleeker								
? Syn-type : No. loc. : Bleeker Coll. Reg. No. B.M. (N.H.) 1880.4.21.119	427	9·47	15·00	6·42	III, 123	i+I+114	33	32+125=157
Eupleurogrammus muticus :								
Trichiurus muticus Gray								
Holotype : India : Hardwicke, Reg. No. B.M. (N.H.) 1955.5.13.2	426	*ca.* 10·26	14·69	*ca.* 7·0	III, 143	i+I+120	41	41+151=192
Eupleurogrammus muticus (Gray)								
No data. Reg. No. B.M. (N.H.) 1955.6.4.1	617	11·21	15·42	7·85	III, 147	i+I+121	42	41+150=191

Bleeker (1860) himself suspected, and Delsman (1927). Delsman goes far towards recognizing the different vertebral counts in *T. muticus* and *T. glossodon*, but in the former case he appears to have had the misfortune to select a specimen with a broken tail and gives 40–115 = 155. De Beaufort comprehends the affinities of *T. muticus* and *T. glossodon*, as he shows in his key, but. apparently not having heard of *Eupleurogrammus*, he retains both species among *Trichiurus* and gives no *Eupleurogrammus* combinations in his synonymies.

De Beaufort's counts on the type material of *T. glossodon* (D.115–120. A. about 90.) seem a little on the low side though, in the nature of the material, not disturbingly so.

Discussion of the relationships of the two species of *Eupleurogrammus* and of their systematic position is continued under the following species.

Eupleurogrammus muticus (Gray)

(Text-fig. 15)

Trichiurus lepturus (part) Linnaeus, 1758, *Syst. Nat.* Ed. 10 : 246 (*fide* Lönnberg *et al.*, 1896, *K. Svensk. Vet.-Akad. Handl.* **22** : 40. See note under *Trichiurus*, p. 114.)
Trichiurus muticus Gray, 1831, *Zool. Misc.* **1** : 10.
Holotype B.M. (N.H.) No. 1955.5.13.2. Type locality India.
Eupleurogrammus muticus, Gill, 1863, *Proc. Acad. nat. Sci. Philad.* **1863** : 226.
Enchelyopus muticus, Bleeker, 1872, *Ned. Tijdschr.* **4** : 131.
non Trichiurus intermedius Gray, 1831, *Zool. Misc.* **1** : 10.

The taxonomy of *Eupleurogrammus muticus* requires very little comment, except a further emphasis on the fact that *T. intermedius* Gray is *not* a synonym of it as Günther has led too many to suppose. I have examined the types of both nominal species and give the results in Table IV. The holotype of *E. muticus* has the gill-covers partly damaged, but another and better specimen has been available also.

It has been discussed whether the distinction holds that *E. muticus* is "burnished silver" and *E. intermedius* "purely silvery"; Delsman and Day *pro*, De Beaufort *con*. De Beaufort appears to clinch the matter when he says:

> "My specimens" (of *muticus*) "do not differ in colour from specimens of *glossodon* '(= *intermedius*)' collected in the same locality and preserved in the same jar."

The type of silver coloration is, in fact, quite variable in any one species of Trichiurid, depending on age, on fixative and preservative, on the amount of oil in the tissues (which can import a golden tinge to the silver) and on the fine or coarse grain of the guanine itself.

Despite the superficial resemblance and absence of a caudal fin it seems surprising that these two species should ever have been placed in *Trichiurus* and still more so that Gill (1863) should have been content to recognize *Eupleurogrammus* without removing it to the *Lepidopodinae*. The typically Lepidopodine palatine teeth and median lateral line are fundamentally different from those of the Trichiurinae; to these characters are allied a rounded operculum and the presence of ventral fins. Further, though the development of the cranial crests is unlike that of *Lepidopus* as of the Trichiurinae, it is very like that of *Evoxymetopon*, a Lepidopodine which Gill had in his hands and classified as such. The dentition of the main series is finer than that of any other genus of the Trichiuridae.

Authors have regarded the ecaudate genera as "degenerate" simply because of their lack of a caudal fin. This is a very hasty and unwise opinion: in fact *Eupleurogrammus* is one of the most advanced. Not only does it display the culminations of a number of progressive trends (see pp. 125-8); in appearance and structure it has the most elegantly streamlined form. The sides of the head and operculum are smoothly curved, with none of that chunkyness which occurs in the more primitive genera; the upper and lower profiles of the body are both gently convex; the dorsal is arched and the always untidy anal entirely suppressed; the point of greatest depth has moved back toward the vent; and a comparison of a radiograph of the skeleton with that of, say *Nesiarchus* or *Diplospinus*, is like a comparison between the mechanism of a high-grade chronometer and of a cheap alarm-clock.

Genus ***ASSURGER*** Whitley

Assurger Whitley, 1933, *Rec. Aust. Mus.* **19**: 84.

Type species *Evoxymetopon anzac* Alexander. Monotypic, Indo-Pacific.

DIAGNOSIS:

(1) Body extremely elongate, head 12 in total length, greatest depth 28 in total length (*ca.* 1415 mm.)

(2) Upper profile of head oblique, rising continuously from the tip of the snout in a straight line set at about 25° to the longitudinal axis and quite straight before the orbits. Structure of cranial crest unknown, but evidently the ethmo-frontal region and the posterior confluence of the frontal crests are both elevated. Interorbital strongly convex.

(3) Orbit small, 8 in head length, $\frac{1}{2}$ an eye-diameter below the dorsal profile

(4) Analysis of dorsal spines and soft rays unknown; aggregate *ca.* 120. First dorsal spine not enlarged.
(5) Anal spines i(?) + I; I is a large oval scale.
(6) Analysis of anal fin elements unknown; only the posterior 14–15 appear to be external fin-supporting rays.
(7) Posterior end of operculum a rounded rectangle, falling about a pectoral base-length short of the pectoral base.
(8) Ventral fins present, scale-like, inserted about 1½ eye-diameters behind the posterior end of pectoral base.
(9) Caudal fin present.
(10) Analysis of vertebrae unknown.

Assurger anzac (Alexander)

(Text-fig. 16 and Pl. 10).

Evoxymetopon anzac Alexander, 1916, *J. Roy. Soc. W. Aust.* **2** : 104, pl. 7.

Holotype in the Western Australian Museum, Perth. Type locality North Fremantle, Western Australia.

Evoxymetopon anzac Kamohara, 1952, *Sci. Rep. Kôchi Univ.* No. **3** : 31, fig. 26.

Assurger alexanderi ("*nom. emend.*, as Anzac is not permissible") Whitley, 1933 ,*Rec. Aust. Mus.* **19** : 84.

(Whitley's emendation is quite unnecessary since a " Recommendation " at the end of Article 14 of the " International Rules of Zoological Nomenclature " expressly states : " Latinized Greek words or barbarous words may, however, be used. Examples . . . *ziczac* . . .")

This species is known from Alexander's original and incomplete description and figure, the latter a photograph showing the head and the trunk back to the level of about the tenth dorsal ray. Whitley, in a general paper of miscellaneous studies, erected *Assurger* apparently on Alexander's account alone and without examination of the specimen which, though remote from Sydney, must surely have been more easily accessible to Mr. Whitley than to any worker outside Australia.

The following are all the data that can be extracted from Alexander :

> " B.7 ; D. *circa* 120 ; A.14 + ; C. 17 ; P. 12.
>
> Total length 1415 mm., length of head 120 mm., greatest height 50 mm., diameter of orbit 15 mm.
>
> " Unfortunately the fins are a good deal broken, and it is impossible to count the rays of either the dorsal or anal with accuracy, no doubt these breakages occurred when it was washed ashore, and if the large spine at the commencement of the dorsal found in *E. poeyi* was ever present it has disappeared. In other respects the example agrees in its structural features with Günther's description, the postanal spine is exposed evidently owing to the abrasion of the skin in that region and just behind it there is a large oval scale similar to that described and figured by Günther. There is no trace of the six narrow reddish bands which Poey describes in *E. taeniatus* and if one may judge from Goode and Bean's figure, the ridge on the forehead is not nearly so high as in that species, but agrees with that of *E. poeyi*." " . . . a bright silvery colour."

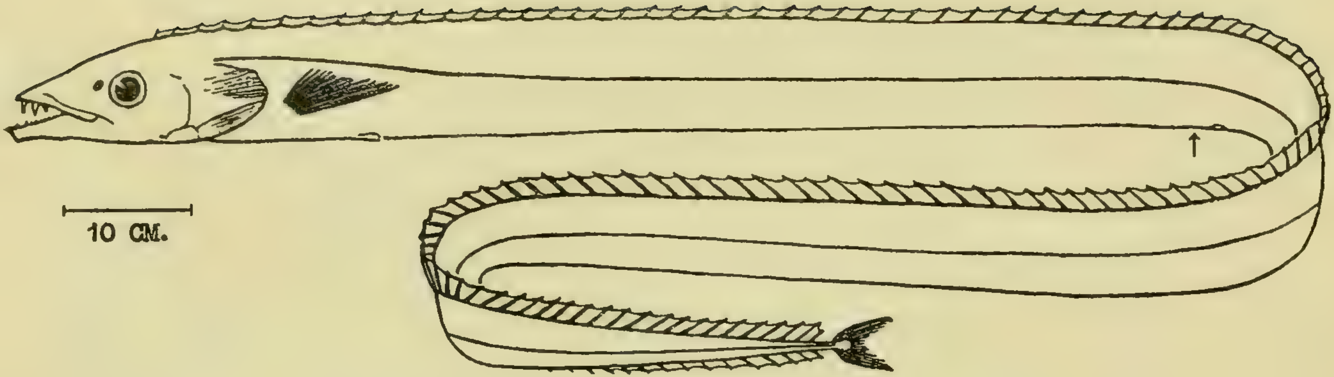

FIG. 16.—*Assurger anzac* (Alexander). Specimen of 2,250 mm. S. L. Japan. (After Kamohara (1952), heavily re-touched.)

Alexander's references are to Poey (1873) and Goode & Bean (1895) (given with other *Evoxymetopon* references on p. 99). Although his discussion mentions Gill (1863) and Günther (1887) also, there is internal evidence in his paper that he cannot have examined them all. Gill clearly states that the type of *E. taeniatus* is nearly five feet long (in which he is followed by Günther) and Poey gives 1410 mm. total length, yet Alexander follows the mistake of Goode & Bean, who copy Gill's percentage proportions of total length as millimetres, and gives 100 mm. as the total length. When, therefore, Alexander denounces Goode & Bean's " very poor figure " of *E. taeniatus* he is complaining of a figure of a fish which he has not seen and which he has not compared with Poey's independent drawing of the same specimen.

Alexander's figure shows the profile of the head rising in practically a straight line from the tip of the snout to behind the eye, the slope (with the mouth open) being about 25° to the longitudinal axis of the body. The eye lies half its diameter from the dorsal profile. The hinder end of the operculum falls about a pectoral base-length short of the pectoral fin. The ventral fins are not mentioned ; the photograph shows a nondescript median projection before the level of the end of the operculum, certainly irrelevant, and a slight indentation, about an eye-diameter behind the pectoral base, which is a likely position for the ventrals but quite inconclusive.

Dr. L. Glauert, Director of the West Australian Museum, has kindly done what he could to amplify Alexander's account. He has provided the original photographic print from which Alexander's plate was made and this is reproduced, I hope with greater clarity than before, as Plate 10 of the present paper. One point which this print does clarify is the fact that there are no barbs on the teeth ; Alexander's plate may seem to indicate a barb on one of the premaxillary fangs, but this is an artifact due to indistinct reproduction of a piece of rubbish on the tooth in question. Dr. Glauert gives the eye-diameter as 16 mm. and the length of the head (measured from the snout-tip) as 113 mm., whence the ratio eye/head-length must be 1/7 instead of 1/8 as given by Alexander. Dr. Glauert is unable to add precision to Alexander's account of the dorsal fin : " . . . a University Undergraduate, interested in fishes, made an attempt and counted only 127, whereas all those others who made the attempt gave from 135 to 142. The explanation is that the dorsal fin was very much damaged when the fish reached the Museum ".

Kamohara (1952) reports one specimen of 2250 mm. from Kôchi Market, Japan, and gives a small figure but no description. The illustration shows the fish bent into an S which prevents measurements of the body proportions and a count of the dorsal fin rays, but the general picture agrees with Alexander's description and figure. One new fact emerges : the ventral fins are inserted about 1½ eye-diameters behind the pectoral base.

Since it is evident that the structure of the ethmoid and frontal region of the head must be similar to that in *Eupleurogrammus* and *Evoxymetopon* I place this fish among the Lepidopodinae, among which it may be considered to parallel *Benthodesmus* among the Aphanopodinae. It is at once separable from *Eupleurogrammus* and *Tentoriceps* by its possession of a caudal fin and from *Lepidopus* by the form of the head and of the elongate body. It differs from *Evoxymetopon* in the gentler slope of the snout, smaller eye (1/7 : 1/6 of the head), elongate body (height 1/28 : 1/12, head

1/12 : 1/8 of total length) and higher dorsal count (*ca.* 120+ : 87). These comparisons are between holotypes of practically identical size (*Assurger anzac* 1415 mm., *Evoxymetopon taeniatus* 1410 mm. total length).

Genus ***TENTORICEPS*** Whitley

Tentoriceps Whitley, 1948, *Rec. Aust. Mus.* **22** : 94.

Type species *Trichiurus cristatus* Klunzinger. Monotypic.

DIAGNOSIS :

(1) Body extremely elongate, head 9 in total length, greatest depth 20–24 in total length (*ca.* 418 mm.)
(2) Upper profile of head convex, a continuous curve rising from the tip of the snout at about 30° to the longitudinal axis and markedly convex before the orbits. Structure of cranial crest unknown, but evidently the ethmofrontal region and the posterior confluence of the frontal crests are both elevated, the former perhaps disproportionately so. Interorbital convex.
(3) Orbit large, 5 in head length (Kluzinger description) or 6 (Klunzinger figure), 2/3 of an eye-diameter below the dorsal profile.
(4) Analysis of dorsal spines and soft rays unknown ; aggregate *ca.* 120. First dorsal spine not enlarged.
(5) Analysis of anal fin elements unknown : " mit rudimentären, kaum sicht-
(6) baren Stachelchen ".
(7) Posterior end of operculum acutely elliptical, reaching to middle of, but not concealing, pectoral base.
(8) Ventral fins present, scale-like, but insertion unknown.
(9) *Caudal fin absent.*
(10) Analysis of vertebrae unknown.

Tentoriceps cristatus (Klunzinger)

(Text-fig. 17).

Trichiurus cristatus Klunzinger, 1884, *Fische Rothen Meeres* **1** : 120, Taf. 13, fig. 5a.

Syntypes retained in Klunzinger's private collection, Stuttgart ; eventual disposal unknown. Type locality Kosseir, Red Sea coast of Egypt.

Tentoriceps cristatus, Whitley, 1948, *Rec. Aust. Mus.* **22** : 94.

All that is known of this species is contained in Klunzinger's original description and figure. I give the complete text :

> " Kopfprofil convex, gratartig, scharf : eine hohe blattartige, bogige Crista zieht vom Beginn der Rückenflosse an über Stirn und Schnauze ; den vorderen Theil der letztern indess nicht mehr schärfend. Das Auge liegt daher weit unter der Profillinie. Bauchflossen wie beim vorigen in Form eines Schuppenpaares wie bei b." (b. is *Trichiurus muticus* Gray, type-species of *Eupleurogrammus.*) " Die Seitenlinie senkt sich sehr allmählig abwärts und läuft etwas über dem unteren Körperdrittel. Afterflosse nur mit rudimentären, kaum sichtbaren Stachelchen. Auge gross, 5 in der Kopflänge, Schnauze von doppelter Länge

> des Auges, Kopf mässig lang, 2¾ mal so lang als der Körper hoch, 9 in der Gesammtlänge. Körperhohe 20–24 (letzteres bei Aelteren) in der Gesammtlänge, Körper also sehr gestreckt. Rückenstrahlen 1 1/4 in der Körperhöhe, 3 1/2 in der Kopflänge, also ziemlich nieder. Brustflossen kurz, 7 in der Kopflänge, (wenn nicht abgebrochen?). Peitsche kurz, nur von 1/2 Kopflänge. Vordere Zähne einfach ohne Ansatz. D. c. 120 (?). Neue Art vom Rothen Meer."
>
> " Von dieser neuen und durch die scharfe, blattartige Kopfgräte gut charakterisirten Art (siehe obige Uebersicht) bekam ich 3 Exemplare bei Koseir, ebenfalls aus dem inneren Meer. Farbe silbrig, Ruckenflosse hyalin ".

The lengths of the three specimens are not given. The head, however, figured " in natürlicher Grösse " is 46·5 mm. in length, (measured from the snout tip) and this multiplied by 9 gives *ca.* 418·5 mm. for the total length of the specimen which is likely to have been the largest of the three.

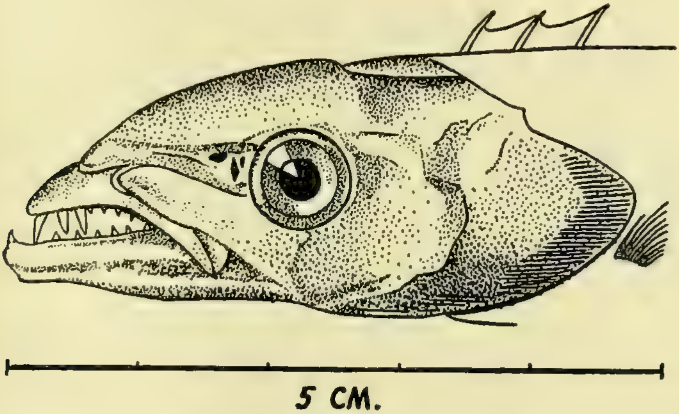

FIG. 17.—*Tentoriceps cristatus* (Klunzinger). Head of syntype *ca* 418 mm. S.L. (re-drawn after Klunzinger (1884), scale added). Some confusion is evident in the representation of the nostrils.

Klunzinger's figure shows only the head, pectoral fin and trunk back to the third dorsal ray. Even so the evidence available appears adequate to justify the recognition of a distinct species and genus, provided it is all accurately related and represented ; relatively small divergences from the published account would involve consideration of possible *Assurger* or *Eupleurogrammus* spp. Klunzinger's careful consideration of the whole genus may justify confidence in his present data.

It is obvious at the outset that *T. cristatus* has very little in common with the Aphanopodinae. It is likewise certain that, despite its ecaudate condition, it differs from the Trichiurinae in the general shape of the head, in the presence of ventral fins, in the median position of the lateral line and the absence of barbs from the teeth. (Elsewhere Klunzinger properly characterises the barbed teeth and falling lateral line in *Trichiurus muticus*).

Considered now as a possible Lepidopodine species *T. cristatus* is quite unlike *Lepidopus*. The form of the upper profile of the head is intermediate between *Evoxymetopon* and *Assurger*, from both of which our species differs in lacking a caudal fin. From Klunzinger's figure it seems that the elevation of the ethmo-frontal region has proceeded further than that of the posterior confluence of the frontal ridges giving an almost teratological appearance which is quite the reverse of the condition in the ecaudate *Eupleurogrammus*. The hind end of the operculum is a rounded point with an extension in relation to the pectoral base intermediate between that in the Aphanopodinae and Trichiurinae and unlike the other Lepidopodines. The number of dorsal rays (*ca.* 120) is similar to that in *Assurger*, but the elongation of the body, though considerable, is slightly less (depth 20–24 : 28 in length). The number of dorsal spines is unknown, likewise the position of the ventral fin-insertions, the condition of the post-anal structures and the number of vertebrae ; nevertheless I find it possible to accept *Tentoriceps cristatus* (Klunzinger) as a valid species and genus arising from a Lepidopodine offshoot a little before *Assurger*.

Whitley (1948) proposes *Tentoriceps* with no more than a translation of Klunzinger's original description of *Trichiurus cristatus*, without any indication of the supposed discriminant characters and with no reference to his own earlier proposal of *Assurger*. He proposes it in a portmanteau paper of " Studies in Ichthyology " having no direct concern with the Red Sea fauna, no special interest in the Trichiuridae nor any Australian material of that family requiring comment. *Tentoriceps* is but another of Mr. Whitley's foundlings, casually discovered, capriciously re-baptized and callously abandoned, in the hope of adoption or decent interment, on the cold doorsteps of systematic ichthyology.

Subfamily TRICHIURINAE Swainson

Trachiurinae (evident misprint for *Trichiurinae*) Swainson, 1839, *Nat. Hist. Fish. Amphib. Rept.* **2** : 254.
Type genus *Trichiurus* Linnaeus.

Lepturinae Gill, 1863, *Proc. Acad. nat. Sci. Philad.* **1863** : 225.
Type genus *Lepturus* Artedi (= *Trichiurus* L.).

Genera now recognised : *Trichiurus* Linnaeus ; *Lepturacanthus* Fowler.

Diagnosis :

A. Slope of snout moderate ; orbits barely entering upper profile of head ; posterior confluence of frontal ridges elevated as a sagittal crest at the nape.
B. Cartilaginous protuberance at mandibular symphysis weak ; a small, soft projection at the tip of the snout.
C. Lower hind margin of operculum more or less concave.
D. Teeth of main series with barbs.
E. Palatine teeth minute, in a villiform band.
F. Lateral line descending steeply from the shoulder and running nearer the ventral surface of the body, i.e. distance between lateral line and ventral profile at anus slightly less than half distance between lateral line and dorsal.

G. Spinous dorsal fin very short, with 3 or 4 rays. Spinous and soft dorsals continuous, without any intervening notch.

H. Soft dorsal rays precisely corresponding with adjacent caudal vertebrae, each basal and interneural element being related to a neural spine.

I. Spinous anal i + I; soft anal rays reduced to internal rudiments or wanting (*Trichiurus*) or taking the form of minute pungent spines which definitely break the ventral profile (*Lepturacanthus*).

J. Anal fin (i.e., basal elements of anal—see I above) extending well beyond dorsal.

K. Caudal fin and hypurals entirely absent.

L. Ventral fins and girdle entirely absent.

M. Pyloric caeca 24, perhaps more.

Osteological literature

Günther, 1860, *Cat. Fish. B.M.* **2** : 343–344. (desc. osteology of *Trichiurus*).
Starks, 1911, *Stanford Univ. Pubs.* No. **5** : 25–26 (desc. general osteology of *Trichiurus*, comp. with *Lepidopus*).
Gregory, 1933, *Trans. Amer. Phil. Soc.* **23** : 316, fig. 195 (skull of *Trichiurus*).

Literature on young stages

Delsman, 1927, *Treubia* **9** : 338.
Lütken, 1880, *K. Dansk. Selsk. Skrift.* **12** : 409.
Nair, 1952, *Proc. Indian. Acad. Sci.* **35B** : 225.
Tang & Wu, 1936, *Lingnan Sci. J.* **15** : 651.

Genus *TRICHIURUS* Linnaeus

Trichiurus Linnaeus, 1758, *Syst. Nat.* Ed. **10** : 246.
Type species *Trichiurus lepturus* Linnaeus *ex* Artedi (see note under *T. lepturus*). Probably monotypic.

Enchelyopus Klein, 1744, *Hist. Piscium* : 51.

Enchelyopus Bleeker, 1862, *Versl. Akad. Amsterdam* **14** : 109.
Type species *Clupea haumela* Forskål. (Also spelt *Encheliopus* by authors. *Non Enchelyopus* Gronovius, 1763).

Gymnogaster Gronovius, 1754, *Mus. Ichth.* **1** : 17.
Type species *Anguilla Jamaicensis* Sloane.

Lepturus Artedi, 1738, *Desc. Spec. Pisc.* : 111.
Type species *Lepturus argenteus* Artedi.

Lepturus Gill, 1863, *Proc. Acad. nat. Sci. Philad.* **1863** : 225.
(*Non Lepturus* Moehring, 1758 ; Brisson, 1760.)

? *Diepinotus* Rafinesque, 1815, *Analyse Nat.* : 91 (*nom. nud.*). (Also spelt *Dipinotus* by authors.)
? *Symphocles* Rafinesque, 1815, *Analyse Nat.* : 91 (*nom. nud.*).
? *Nemochirus* Rafinesque, 1815, *Analyse Nat.* : 91 (*nom. nud.*).

DIAGNOSIS :

(1) Body-proportions highly variable : Head 7·0–9·4 in length, depth 14·4–21·0 in length.

(2) Eye relatively large, 5·0–7·0 in head.

(3) Dorsal spines III ; D.III, 137 in three specimens of three nominal species radiographed. (Published aggregate ranges D.120–140).

(4) A. i + I + 105–108.

(5) Post-anal scute (= anal spine I) not enlarged ; a small, triangular scale, less than the pupil.

(6) First basal element of anal fin slightly enlarged, presumably a compound of 2, its interhaemal spine lengthened and slightly thickened. There follows a gap of 1 in the series of interhaemal spines, leaving 1 free haemal arch.

(7) " Soft anal " elements minute spinules which usually do not break the skin and which are occasionally absent. The first *ca.* 60 are directed backwards, the last *ca.* 40 are directed forwards.

(8) Vertebrae 39–40 + 123–128 = 162–168.

Probably only one variable species, *Trichiurus lepturus* L., world-wide except in colder regions.

Trichiurus lepturus Linnaeus

(Text-fig. 18).

Trichiurus lepturus (part) Linnaeus (ex Artedi), 1758, *Syst. Nat.* Ed. **10** : 246.

Type in the Museum of the Royal University of Upsala. Type locality South Carolina. *Note.*—Lönnberg *et al.*, 1896, *K. Svensk. Vet.-Akad. Handl.* **22** : 40, state that the Linnaean types of " *T. lepturus* " at Upsala include material of the species now known as *Eupleurogrammus muticus* (Gray). The suggestion that *T. lepturus* should consequently be replaced by *T. argenteus* Linnaeus, 1754, *Mus. Ad. Frid.* : 76, pl. 26, fig. 2 is, of course, illegal, nor is it really necessary since the situation has never created any practical difficulty.

Günther, 1898, *Proc. Linn. Soc. Lond.* **1898–9** : 29, satisfied himself that the Linnaean material in the possession of the Linnaean Society of London is, in fact, *T. lepturus*, which is rendered doubly certain by the fact that it came from Garden's South Carolina collections, consignment of 1761. (See also *id. ib.* : 25.)

Trichiurus lepturus J. L. B. Smith, 1949, *Sea Fish South Africa* : 313 ; Okada, 1955, *Fishes of Japan* : 155.

Trichiurus argenteus Shaw, 1803, *Gen. Zool.* **4** : 90, pl. 12 (apparently *ex* Linnaeus, 1754).

Clupea haumela Forskål, 1775, *Descr. Anim.* : 72.

Type *not* in Herbarium Ichthylogicum Forskalii, Copenhagen (*fide* N. B. Marshall, personal communication). Type locality Red Sea.

Trichiurus hamrela Schneider, 1801, *Syst. Ichth.* : 518 (*nom. err.*).

Trichiurus lepturus japonicus Temminck & Schlegel, 1844, *Faun. Jap. Pisc.* : 102, pl. 54.

Type Leiden Museum No. 2040. Type locality Japan.

Trichiurus lepturus japonicus Boeseman, 1947, *Zool. Meded.* **28** : 96 (for Temminck co-author p. 2).

Trichiurus japonicus Bleeker, 1857, *Verh. Bat. Gen.* **26** : 98.

Trichiurus japonicus Lin, 1936, *Bull. Chekiang Fish. Sta.* **2** (5) : 2.

Trichiurus lajor Bleeker, 1854, *Nat. Tijdschr. Ned. Indie* **7** : 248.

Type in Leiden Museum. Type locality Manado, Celebes. (Re-examined by De Beaufort, 1951, *Fish. Indo-Austr. Archip.* **9** : 196.)

Trichiurus malabaricus Day, 1865, *Proc. zool. Soc. Lond.* **1865** : 20.

Holotype B.M. (N.H.) No. 1867.5.30.2. Type locality Madras. (Withdrawn as *T. haumela* by Day, 1876, *Fish. India* : 201.)

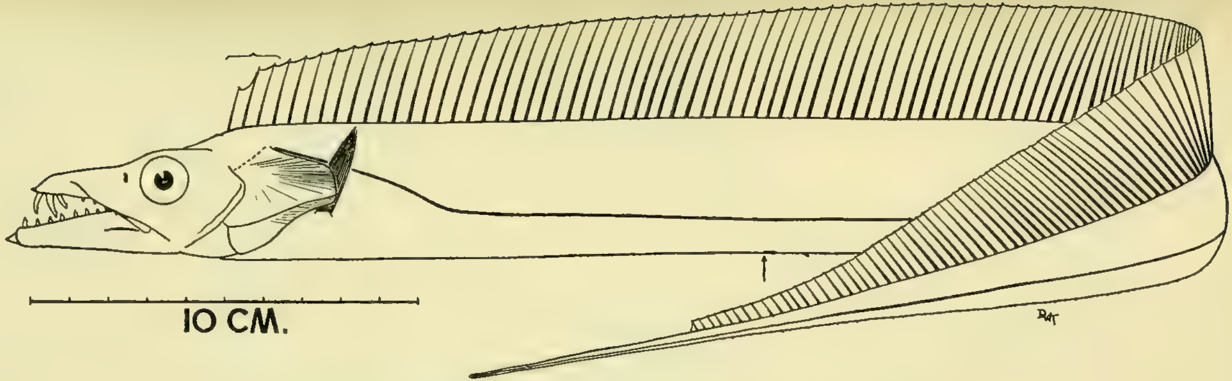

FIG. 18.—*Trichiurus lepturus* Linnaeus. B.M. (N.H.) No. 1948.8.6.795.
Texas. 545 mm. S.L.

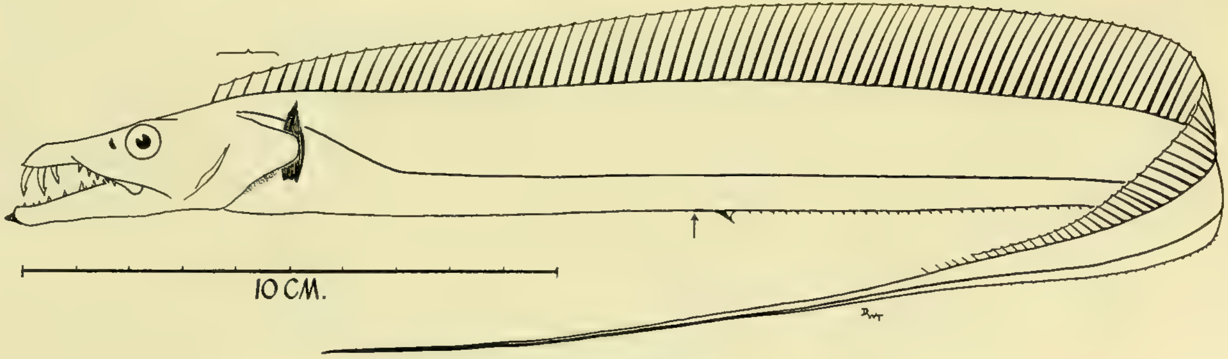

FIG. 19.—*Lepturacanthus savala* (Cuvier). 406 mm. S.L.
(Holotype of *Trichiurus armatus* Gray.)

Trichiurus auriga Klunzinger, 1884, *Fische Rothen Meeres* **1** : 120, Pl. 12, fig. 1.
Type retained in Klunzinger's private collection, Stuttgart. Now at Stuttgart, Berlin or Vienna ? Type locality Kosseir, Red Sea coast of Egypt.
Trichiurus auriga Weber, 1913, *Siboga Fische* : 406.
Trichiurus auriga De Beaufort, 1951, *op. cit.* : 196.
Trichiurus coxii Ramsay & Ogilby, 1887, *Proc. Linn. Soc. N.S.W.* **1887 2** (2) : 562.
Holotype Australian Museum, Sydney No. I.1342. Type locality Broken Bay, N.S.W.
? *Trichiurus nitens* Garman, 1899, *Mem. Mus. comp. Zool. Harv.* **26** : 69.
Syntypes (2) in U.S. N.M. ? Type locality coast of Peru.
? *Trichiurus nitens* Hubbs & Hubbs, 1941, *Calif. Fish Game* **27** : 29.
? *Trichiurus nitens* Breder, 1936, *Bull. Bingham Ocean. Coll.* **2** Art. 3 : 12.
non Trichiurus lepturus Mohr, 1786, *Forsøg til en islandsk Naturh. Kjob.* : 63.
non Trichiurus lepturus Sveinn Palsson, 179+, *J. Naturforsk. Reise Island* 1791–97 **2**.
(Mis-identifications of *Trachypterus* sp. Refs. *fide* Saemundsson, 1926, *Fiskarnir* : 155. Reykjavík).
non Trichiurus lepturus Hoy, 1815, *Trans. Linn. Soc. Lond.* **11** : 210–212.
(Mis-identification of *Trachypterus* or *Regalecus* spp.)
non Trichiurus trimaculatus Giovene, 1829, *Mém. Soc. Ital.* **20** Pt. 1 : 25.
(Mis-identification of *Trachypterus* sp.)

At the commencement of the present paper *Trichiurus* seemed likely to give the most difficulty ; that promise has been abundantly fulfilled. *Trichiurus* is a common pelagic fish of world-wide distribution, occurring in all but the coldest seas and assuming some economic importance in certain areas ; as a consequence it possesses a literature as large as that of the rest of the family put together. Much of this work is uncritical : species have been recognized on supposed differences of body-proportions unrelated to possible ontogenetic changes, geographic variation, or environmental effects, or on small differences in fin-ray counts which are difficult to establish with any accuracy except in radiographs. Vertebral counts have hardly ever been employed. Very often it is found that where a worker has characterised a pair of species to his own satisfaction another will reverse the discriminant characters in the same pair.

In dealing with all this intractable material it has seemed useful to take as a working hypothesis the theory that we are dealing with one highly variable species. If the evolutionary behaviour of the other recent Trichiuridae affords any precedent it is one pointing to the evolution of monotypic genera, or of pairs of species having sharply discontinuous ranges of meristic counts, not to the subtle distinctions which the would-be splitters of *Trichiurus* postulate. Geographic variation and the increasing evidence of environmental effects upon meristic characters must also be taken into account.

The first problem is the identity or distinctness of the Atlantic and Indo-Pacific populations; currently recognized as *T. lepturus* L. and *T. haumela* (Forskål) respectively. The results of the examination of two specimens taken at random from the collections of the British Museum (Natural History) are given in Table V. They show a precisely coincident dorsal count and anal/vertebral counts differing by only 3/2 rays/vertebrae respectively. The differences in body proportions are no greater than may be explained by the difference in age. These two specimens show that similar *Trichiurus* occur off Texas and Shanghai almost as well as population samples treated with all the apparatus of statistical necromancy.

TABLE V.

	Trichiurus lepturus. Aransas Bay, Texas. No. 1948.8.6.795.	*Trichiurus "haumela."* Shanghai. No. 1862.11.1.260.	*Trichiurus "japonicus."* Yenting, Chekiang. No. 1925.4.23.5.
Dorsal rays	D.III, 137	D.III, 137	D.III, 137
Anal rays	A.i+I+105	A.i+I+108	A.i+I+107
Vertebrae	39+123=162	40+124=164	40+128=168
Standard length	545 mm.	838 mm.	926 mm.
Head in S.L.	7·07	7·83	9·17
Depth in S.L.	16·03	16·43	17·47
Snout-vent in S.L.	2·79	3·07	3·07
Head in S-V.	2·53	2·55	2·98
Depth in S-V.	5·73	5·35	5·68
Eye in head	5·92	6·68	6·12
Snout in head	2·80	2·77	2·52
Mx. in head	2·48	2·46	2·29

A modern re-assessment of *Trichiurus japonicus* Temminck & Schlegel, a second Pacific form, is given by Boeseman (1947):

> "The differences between *Trichiurus japonicus* T. & S. and *T. lepturus* L. as stated by Temminck & Schlegel and Bleeker (*l.c.*) do not exist in our material. A comparison, however, with several specimens of *lepturus* in our collection (all Atlantic) showed a very distinct and constant difference; the head in all these specimens of *lepturus* is larger, about 7–7·5 in length, while in our specimens of *japonicus* it is 8·1–8·6 in length, consequently considerably smaller. On account of this I want to discriminate both species and regard the Japanese specimens as the type material of a separate species, *Trichiurus japonicus* T. & S. Specimen no. 2040 I regard as type."

In opposition to this stands the work of Lin (1936) who comments that:

> "Several authors . . . used to distinguish *T. japonicus* from *T. haumela* by the shorter head and the smaller eyes, but the series of intermediate forms lying between them is so continuous that no clear line can be drawn to separate them into two distinct species."

Lin gives a table of data covering a series of 12 Chinese *T. japonicus* of 424–1,290 mm. S.L., with the following ranges: depth in length 14·4–21; head in length 7–9·4; depth in head 1·9–2·3; eye in head 5·4–6·4; D.136–140. He notes the difficulties which arise through the loss of the tip of the tail and advocates the substitution of snout-vent length for the calculation of body-proportions. Oddly enough Lin does not take the logical step of substituting the earlier name *haumela* for *japonicus*.

> "In reviewing the recorded distribution of *T. japonicus* and *T. haumela*, it is found that the former species inhabits the Chinese and Japanese coastal waters and is neither known to live beyond the Asiatic continental shelf nor

> southward to the East Indian seas, while the latter is found from the Japanese and Chinese seas to the Philippines and Indian Ocean and Archipelago."

A specimen of *T. japonicus* (Table V), being duly radiographed, shows a dorsal count identical with that of the two specimens of the other two nominal species, an intermediate anal count and an increment in caudal vertebrae altogether less than the head/body proportion would lead one to expect. I suggest that *T. japonicus* is, in the light of the evidence, no more than an ecotypic form of *T. haumela* (= *lepturus*).

T. lajor Bleeker and *T. malabaricus* Day have been adequately dealt with by De Beaufort (1951) and by Day himself (1876) and as synonyms of *T. haumela* now need no further comment.

T. auriga Klunzinger, placed very close to *T. haumela* by Klunzinger (1884) himself and founded on a very young specimen (250 mm. S.L.) is probably no more than a juvenile of the latter species, though the published illlustration contains peculiar features at variance with the description. The only serious difficulty is the definitely stated absence of barbs from the teeth. *T. auriga* has been reported only once more, a specimen of 320 mm. from the Timor Sea having been described by Weber (1913) and De Beaufort (1951).

T. coxii Ramsay & Ogilby (1887) contains, on the published account, no differences from *T. haumela* and its authors do not attempt to indicate those characters in which they consider it to be divergent.

Only in the case of *T. nitens* Garmen (1899) has there been argued any very cogent case for specific separation, by Breder (1936) and by Hubbs & Hubbs (1941). Breder's conclusions, summarized in the form of a key are:

A. Dorsal rays never less than 126, usually about 133 ; maxillary 2·2 to 2·5 in head, usually about 2·3 (11 specimens, D.126–137, mean 132·9) . . . *lepturus* Atlantic

AA. Dorsal rays never more than 128, usually about 122 ; maxillary 2·5 to 2·8 in head, usually about 2·6 (36+ specimens, D.120–128, mean *ca.* 122·3 *nitens* California, Galapagos

These results must obviously be treated with respect, though not with absolute aquiescence. The variation in the maxillary should be stated in relation to the size of the fish, for there is some allometry with age. The differences in mean dorsal counts are considerable, but if the two samples are drawn from a continuous hypothetical population of one species, having its origin somewhere in the Indian Ocean and extending westwards to the Western Atlantic and eastwards to the Pacific coast of America we still have no more than the variation we should expect at the limits of that wide range. The satisfactory establishment of *T. nitens* requires, not comparison with Atlantic material, but demonstration of a non-cline discontinuity across the Pacific.

Having regard therefore to the known variation in the Trichiuridae and to the growing literature concerning environmental effects upon fishes, I am more inclined to " lump " *Trichiurus* as one variable species than to " split " and thereby make assumptions concerning the genetic distinctness of populations which present precedents and evidences of variation do not appear to justify. Such modern authors as J. L. B. Smith (1949) and Okada (1955) have apparently arrived at the same conclusion, though they do not submit any evidence to support their decisions.

Genus *LEPTURACANTHUS* Fowler

Lepturacanthus (sub-genus of *Trichiurus* L.) Fowler, 1905, *Proc. Acad. nat. Sci. Philad.* **1904** : 770.

Type species *Trichiurus savala* Cuvier. Monotypic.

Trichiurus (part) many earlier authors.

DIAGNOSIS :

(1) Body-proportions highly variable : Head 7·4–10·5 in length, depth 14·8–19·8 in length.
(2) Eye relatively small, 6·7–10·0 in head.
(3) Dorsal spines IV ; D.IV, 111 in two specimens radiographed, including holotype of *Trichiurus armatus* Gray. (Published aggregate ranges D.105–134).
(4) A.i + I + 72.
(5) Post-anal scute (= anal spine I) enlarged, as in *Aphanopus* ; a dagger-like spike half the diameter of the eye.
(6) First basal element of anal fin markedly enlarged, as in *Aphanopus*, presumably a compound of 3, its interhaemal spine likewise lengthened and thickened. There follows a gap of 2 in the series of interhaemal spines, leaving 2 free haemal arches.
(7) " Soft anal " elements pungent spinules, definitely breaking the ventral profile throughout the length of the fin and all directed backwards.
(8) Vertebrae 32–35 + 124–130 = 159–162.

One species, *Lepturacanthus savala* (Cuvier). Indo-Pacific.

Lepturacanthus savala (Cuvier)

(Text-fig. 19).

Trichiurus savala Cuvier, 1829, *Règne Animal* 2 Ed. **2** : 219.

Syntypes in Paris Museum, Reg. No. a.5357–5358. Type locality " Mer des Indes " (= Bombay & Malabar).

Trichiurus (*Lepturacanthus*) *savala* Fowler, 1905, *Proc. Acad. nat. Sci. Philad.* **1904** : 770.

Trichiurus armatus Gray, 1831, *Zool Misc.* **1** : 9 ; Gray, 1835, *Illust. Ind. Zool.*, pl. 93, fig. 1.

Holotype B.M. (N.H.) No. 1955.5.13.1. Type locality India.

Trichiurus Roelandti Bleeker, 1860, *Acta Soc. Indo-Neer.* **8** (4) : 30.

Holotype in Leiden Museum. Type locality Sunda Strait. (Re-examined by De Beaufort, 1951, *Fish. Indo-Austr. Archip.* **9** : 194.)

Trichiurus armatus Gray has for long, and, for once, correctly, been regarded as a synonym of this species. De Beaufort has adequately dealt with *T. Roelandti* Bleeker and so the taxonomic situation in this newly-promoted genus *Lepturacanthus* is mercifully straightforward.

Lepturacanthus is obviously closely related to *Trichiurus* and as widely separated from the other Trichiuridae : any attempt at a natural classification must adequately express this situation. In a wide classification Fowler's erection of *Lepturacanthus* as a sub-genus of *Trichiurus* very adequately did so, but with the exposure of *Eupleurogrammus* and its removal to the Lepidopodinae the Trichiurinae are left as a very small group. Within this group the divergence between *Lepturacanthus savala* and *Trichiurus lepturus* is very comparable to that between *Aphanopus* and *Benthodesmus* and accordingly consistency requires the elevation of *Lepturacanthus* to full generic status.

THE ORIGIN, EVOLUTION AND CLASSIFICATION OF THE TRICHIURIDAE

Summary of earlier work

Before summarizing previous opinions on the classification of the Trichiuridae it may be useful to indicate the sequence of recognition of the genera now accepted :

Trichiurus	Linnaeus,	1758.
Lepidopus	Gouan,	1770.
Aphanopus	Lowe,	1839.
Evoxymetopon	(Poey) Gill,	1863.
Eupleurogrammus	Gill,	1863.
Benthodesmus	Goode & Bean,	1882.
Lepturacanthus	Fowler,	1905.
Assurger	Whitley,	1933.
Diplospinus	Maul,	1948.
Tentoriceps,	Whitley,	1948.

Classification commences, and commences remarkably well, with Cuvier & Valenciennes (1831) who recognize the Scombroids as a natural group (Scombéroïdes) containing all the Trichiurids and Gempylids so far known (Lépidopes, Trichiures ; Thyrsites, Gempyles) as well as the Tunnies, etc. Their key runs :

> " *Tous ou une grande partie des rayons de l'anale réduits à de très-petites épines.*
> Dents des thyrsites et des gempyles.
> Lépidopes. Une petite écaille au lieu de chaque ventrale ; une caudale.
> Trichiures. Point de ventrales ; point de caudale."

These authors grasp so early the essential relationships of the Trichiuridae and Gempylidae :

> " Il est impossible de ne pas placer à la suite des gempyles et des thyrsites deux genres de poissons qui leur ressemblent presque en toutes choses, si ce n'est qu'ils manquent entièrement de fausses nageoires et même de rayons mous à leur dorsale ; ce sont les lépidopes et les trichiures, poissons très-remarquables d'ailleurs par leur éclat et par leurs formes singulières.
>
> " Leur tête, leurs dents, leur peau, leur squelette, rappellent de tout point les genres auxquels nous les associons, et la longueur même de leur corps en ruban, qui les avait fait rapprocher des cépoloïdes, est déjà annoncée par la forme de plusieurs gempyles."

Swainson (1839) was the first to erect a higher taxon for the Trichiurid fishes, though he takes a step backwards, making *Ammodytes* as well as *Trichiurus* and *Gempylus* members of a sub-family Trichiurinae of the family Coryphaenidae.

Günther (1860) attempts no subdivision of his family Trichiuridae, which includes not only *Aphanopus*, *Lepidopus* and *Trichiurus* but also the Gempylids *Epinnula*, *Dicrotus*, *Thyrsites* and *Gempylus*.

Gill (1863) gives a classification recognizably approaching that now advocated, though based on inadequate and in part inaccurate premises :

" I. Dorsal fin undivided.	
A. Tail filiform and finless	LEPTURINAE.
Lateral line near the abdomen	*Lepturus*.
Lateral line median	*Eupleurogrammus*.
B. Tail with a normally developed and forked fin	LEPIDOPODINAE.
Profile rectilinear and forehead depressed	*Lepidopus*.
Profile high, trenchant and boldly declining	*Evoxymetopon*.
II. Dorsal fin double	APHANOPODINAE.
Teeth of the palate wanting	*Aphanopus*.

Johnson (1865) describes a number of Gempylids as Trichiuridae.

Capello (1868) takes a view of the Trichiuridae equivalent to the Trichiuriformes of later authors and recognizes three sub-families :

TRICHIURINA	*Trichiurus*, *Eupleurogrammus*. *Lepidopus*, *Evoxmyetopon*. *Aphanopus*.
GEMPYLINA	*Gempylus*, *Prometheus*, *Epinnula*.
THYRSITINA	*Thyrsites*, *Dicrotus*.

A division of the Trichiurina similar to Gill's is implicit in the key given. Time, on the whole, has dealt more kindly with Capello than did Günther in the *Zoological Record*.

Goode & Bean (1895) limit the Trichiuridae to *Trichiurus*, of which *Eupleurogrammus* is merely " a Chinese form . . . with a single species "! They erect a separate family, the Lepidopidae, with two sub-families :

" I. Dorsal continuous. Teeth on palatines. Ventrals present, scale-like, rudimentary. No post-anal spine	LEPIDOPINAE.
(Genera *Lepidopus*, *Evoxymetopon*, *Benthodesmus*.)	
II. Dorsal in two subequal portions, closely contiguous. No teeth on palatines. Ventrals absent. A dagger-like post-anal spine	APHANOPINAE.
(Genus *Aphanopus*.)	

This pastiche of half-truth and etymological abomination is preceded by one of Goode & Bean's self-contradictions (Lepidopidae have " No teeth on palatines "; Lepidopinae have " Teeth on palatines ").

Boulenger (1904) and Goodrich (1909) include both Trichiurids and Gempylids in a family Trichiuridae without subdivisions. This grouping becomes the Scombroid Division Trichiuriformes of Regan (1909), with two undivided families Trichiuridae and Gempylidae in the generally accepted modern sense, as later followed by Jordan (1923) and by Berg (1940).

Starks (1911), in a classic paper concerned only with the osteology of three genera, defines families Gempylidae (*Promethichthys*), Lepidopidae (*Lepidopus*) and Trichiuridae (*Trichiurus*). He comments that " the descent of the family Trichiuridae from the Gempylidae was long ago pointed out " and compares the structure of *Lepidopus* with that of *Promethichthys*, which latter he rightly regards as too specialized to be an ancestral form. He concludes : " This ancestor may have been *Gempylus*, a form which I have been unable to obtain, but showing a development towards the elongate forms of *Lepidopus* and *Trichiurus*."

Roule (1927) introduces a little light relief by attempting to place the Iniomous *Anotopterus* among the Trichiuridae.

Gregory (1933) figures a museum exhibit showing in pictorial form the evolution of the Scombroid fishes. *Ruvettus*, *Epinnula*, *Gempylus* and *Trichiurus* are shown as consecutive stages in a linear series, with *Lepidopus* emerging as a sideshoot between *Epinnula* and *Gempylus*. In these circumstances the presence of a number of apparently undecided fishes swimming in the background to this exhibit occasions no surprise.

Tucker (1953), though not attempting a full classification, draws attention to the affinities between *Aphanopus* and *Benthodesmus* as contrasted with *Lepidopus*. He shows that *Benthodesmus* has a differentiated and partly divided dorsal fin like that of *Aphanopus* and demonstrates the significance of the ventral fin-insertions and post-anal structures, but, fails to realize that the dorsal fin is differentiated throughout the entire family. The error arose through an undue reliance on previous literature of the non-Aphanopodinae and a brief study of *Lepidopus* and *Trichiurus* from radiographs which, for reasons of economy, were fragmentary. Dr. Carl L. Hubbs, *in litt.* kindly drew attention to this mistake.

Nesiarchus-Diplospinus : *the Gempylid-Trichiurid bridge*

Regan (1909) gives the following diagnosis of the Gempylidae which may still serve as a basis for comparison with the Trichiuridae (p. 74) :

> " Body oblong or elongate, compressed ; maxillary exposed ; spinous dorsal longer than the soft ; anal with 3 spines, similar to the soft dorsal ; each pelvic fin of a spine and 5 soft rays or reduced to a spine only ; caudal fin present. Rays of the spinous dorsal equal in number to the vertebrae below them, each interneural usually attached to a neural spine ; rays of soft dorsal and anal more crowded (except the isolated finlets, when present), about twice as numerous as the corresponding vertebrae ; pelvic bones separate, anteriorly extending forward to the cleithra and firmly imbedded in the ligament between them. Vertebrae 31(15 + 16) to 53(28 + 25) ; anterior praecaudals without parapophyses, with sessile ribs ; posterior praecaudals with ribs attached at the extremities of closed haemal arches ; epipleurals attached to the centra."

Closely related to the Scombridae, from which, however, they may be descended by more than one line, the Gempylidae are quite a varied group of fishes. As Mrs. Grey (1953) notes :

> " There is a puzzling scattering of such characters as the presence of a free dagger-shaped spine preceding the anal fin, of dorsal and anal finlets, double or single lateral lines ; and the presence, absence, or reduction of ventral fins."

A goodly proportion of the genera are well-illustrated in the paper by Matsubara & Iwai (1952).

The ancestors of the Trichiuridae must undoubtedly be sought among the Gempylinae (*Gempylus* Cuvier, *Nesiarchus* Johnson, *Mimasea* Kamohara), Gempylidae which possess an especially elongate body, the head and trunk in particular being reminiscent of those of the Trichiurids although the tail seems greatly telescoped by comparison and curiously unfinished. In these three genera alone appear the conical cartilaginous processes at the tip of the snout and mandibular symphysis which are found in the Aphanopodinae ; their skulls are long and low, without prominent crests ; they have, like other Gempylids, the typical Trichiurid dentition with the three pairs of prominent premaxillary fangs ; their squamation is, at the most, vestigial, leading directly to the naked bodies of the Trichiuridae.

A single row of teeth is present on the palatine in *Nesiarchus* (personal observation) and in *Gempylus* (Matsubara & Iwai), though *Mimasea* is said to have none.

Of these three Gempyline genera *Mimasea* (Text-fig. 20) is specialized in having a double lateral line and a ventral fin-insertion behind the pectoral base ; primitive in that the ventral fin is quite well developed, with five soft rays. Despite low median fin-ray counts and presumably low vertebral counts therefore, it does not seem a likely ancestor to the Aphanopodine Trichiurids.

Gempylus (Text-fig. 21) has rather less well-developed ventrals, allied, however, to a double lateral line and a series of widely-spaced dorsal and anal finlets. The proportion of soft dorsal rays to aggregate vertebrae in this genus is very low (18 : 53) in comparison with *Diplospinus*, the most primitive recent Trichiurid (40 : 58) and, since the early history of the Trichiurids appears to show soft dorsal rays multiplying much faster than the caudal vertebrae, we may feel that the transition from 53 to 58 vertebrae represents a smaller change than is likely to admit the necesary concomitant structural changes (Table VI).

Nesiarchus, (Text-fig. 22) however, seems to stand very close to the primitive Trichiuridae. It has a total of vertebrae (35) near to the minimum of its family (31 in *Epinnula*), allied to a higher number of soft dorsal rays than in *Gempylus* (21–23 : 18) and without detached finlets. The ventral fins are inserted on the perpendicular through the posterior end of the pectoral base and consist each of a spine with four smaller soft rays. The skull is well figured by Steindachner (1867) ; apart from a broad general resemblance to the skulls of the Aphanopodinae there is a striking similarity in the deep opercular notch, nowhere as marked in the other Gempylidae and found in only one Trichiurid—the primitive *Diplospinus*. The post-anal spines appear superficially "wrong" ; the first is much larger. But internally there is a rudiment of yet another before the first ; there are three well-developed spines in *Epinnula* and it becomes evident that of these the first is to become the minute spinule of *Nesiarchus* and the Trichiuridae (i), the second will become the larger spine of *Nesiarchus* and the principal spine or scute of the Trichiuridae (I), and the third, though disappearing, is to signify its claim by a space in the anal fin and will contribute to the compound and reinforced anterior basal structure whenever this is developed.

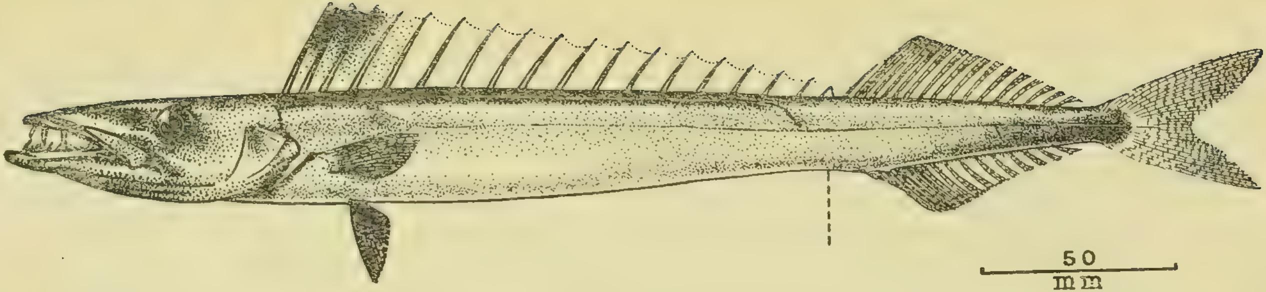

FIG. 20.—*Mimasea taeniosoma* Kamohara. 280 mm. S.L. Japan (from Matsubara & Iwai, 1952).

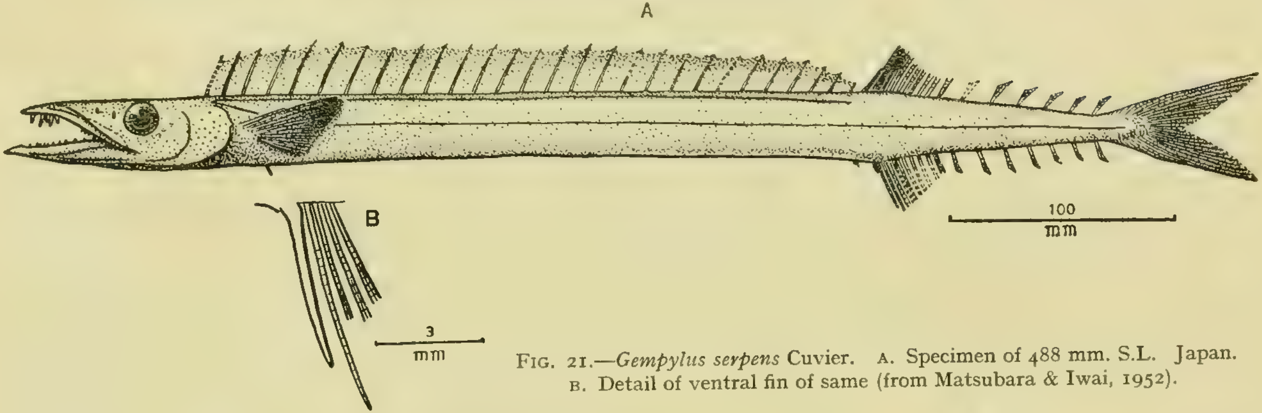

FIG. 21.—*Gempylus serpens* Cuvier. A. Specimen of 488 mm. S.L. Japan. B. Detail of ventral fin of same (from Matsubara & Iwai, 1952).

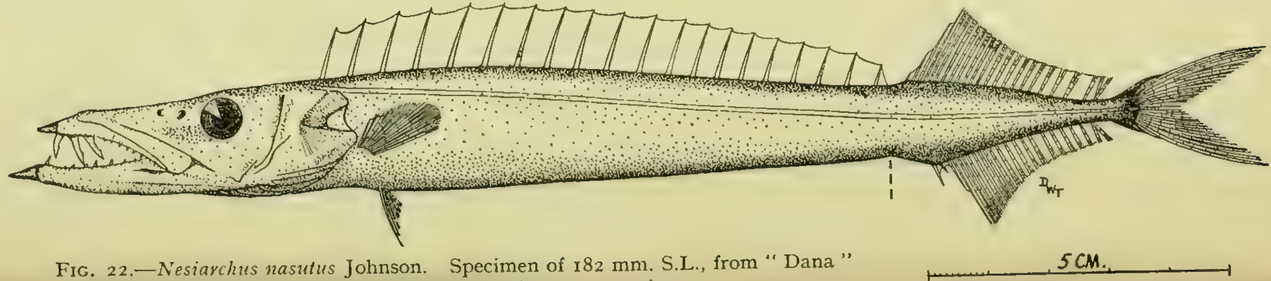

FIG. 22.—*Nesiarchus nasutus* Johnson. Specimen of 182 mm. S.L., from " Dana " St. 1186V., 17° 54′ N., 64° 54′ W., 1,000 m. wire.

The body of *Nesiarchus* is quite naked; the lateral line is single and descends gently to a mid-lateral course along the caudal. The number of pyloric caeca (7) is similar to that in the Aphanopodinae.

Nesiarchus differs from *Diplospinus* in the lower meristic counts, in having the maxillary exposed, in having barbs on the teeth confined to the premaxillary fangs and in the external (though not in the internal) structure of the spinous anal fin. But the indications from a study of the subsequent evolution of the Trichiuridae are that during the addition of 18 vertebrae *Nesiarchus* would have had plenty of time to undergo the modifications needed to produce a *Diplospinus*. This is the view expressed in Text-fig. 23.

Nesiarchus and *Diplospinus* therefore may be regarded as the approaches to the Gempylid-Trichiurid bridge. Whether the Trichiurinae crossed by the same bridge or by a parallel bridge further downstream is still debatable. It is tempting to regard the low lateral line in the Trichiurinae as representing the lower limb of the fork in another Gempylid ancestor; but unfortunately, although *Trichiurus* has a longitudinal groove which would serve for an upper limb, no recent Gempylid has a lower limb which falls in quite the same way. If, however, the " toothless " palatines in *Mimasea* should, on further examination, prove to be provided with a villiform band of teeth, the discovery would be a significant indication of a possible relationship and therefore of a diphyletic descent of the Trichiuridae. In this connexion it is interesting to observe that the concave lower hind margin of the operculum, characteristic of the Trichiurinae (though not of *Nesiarchus*, the Aphanopodinae or the Lepidopodinae), makes sporadic appearances among the primitive Gempylidae in *Epinnula* and *Neoepinnula*.

Evolutionary trends in the Trichiuridae

Evolution in the Trichiuridae has resulted from the action, at various rates, of the following trends:

(1) Elongation of the caudal region of the body, least in the stem-forms at any level (*Diplospinus*, *Lepidopus*) and greatest in the most divergent side-shoots (*Benthodesmus*, *Assurger*, *Tentoriceps*).

(2) Multiplication of the soft dorsal and anal rays, initially at a greater rate than that of the adjacent vertebrae. This development, already incipient throughout the Gempylidae, is seen proceeding at its greatest rate in *Diplospinus* and is practically in harmony with the multiplying vertebrae in the other Aphanopodinae.

(3) Multiplication of the caudal vertebrae until eventually (except at the caudal tip) each vertebra has one corresponding soft dorsal and anal ray with their associated basal elements. This process is nearly complete in *Aphanopus* and *Benthodesmus*, in which, however, there are usually a very few rays, mainly towards the beginning and end of the soft fins, which are not directly related to vertebrae. Except possibly in " *Lepidopus xantusi* " further additions of vertebrae and fin rays proceed in unison in the Lepidopodinae and Trichiurinae.

(4) A slower increase in the number of trunk vertebrae. (See Table VI in conjunction with Text-fig. 23).

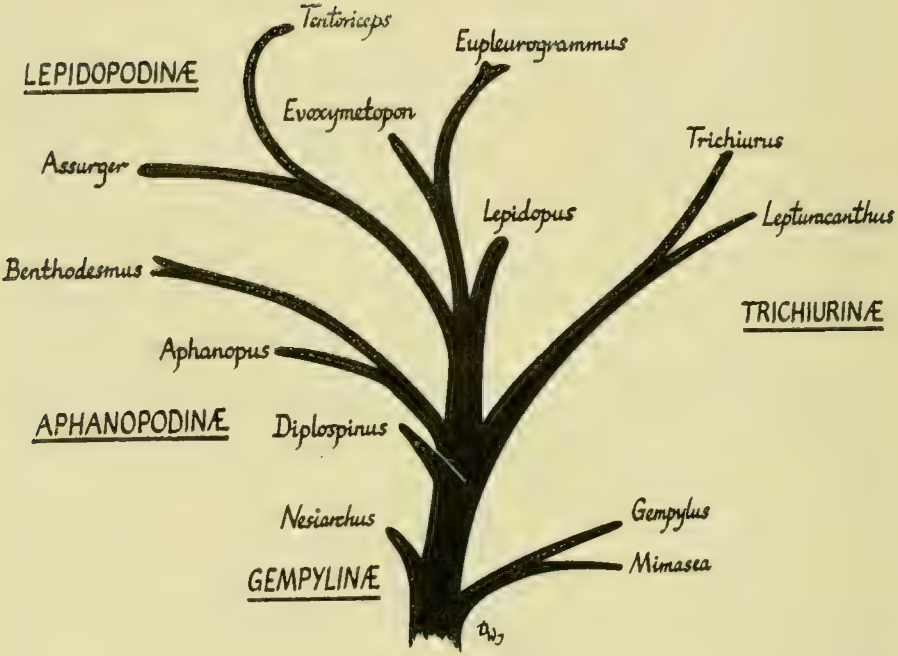
Tentoriceps
Eupleurogrammus
LEPIDOPODINÆ
Evoxymetopon
Trichiurus
Assurger
Lepidopus
Lepturacanthus
Benthodesmus
TRICHIURINÆ
Aphanopus
APHANOPODINÆ
Diplospinus
Nesiarchus
Gempylus
Mimasea
GEMPYLINÆ

FIG. 23.—Suggested relationships of the genera of the Gempylid subfamily Gempylinae and of the subfamilies and genera of the family Trichiuridae.

TABLE VI.

	Dorsal.		Vertebrae.
	Spines.	Soft rays.	
GEMPYLIDAE			
Gempylinae :			
Nesiarchus nasutus	19–21	21–23	23+12=35
Mimasea taeniosoma	18	16–18	—
Gempylus serpens	29–32	18	53
TRICHIURIDAE			
Aphanopodinae :			
Diplospinus multistriatus	32–33	40	34+24=58
Aphanopus carbo	38–41	53–56	42–44+55–56=98–99
Benthodesmus tenuis	39–42	80–88	47–52+75–80=123–131
Benthodesmus simonyi	45–46	102–108	52–53+101–103=153–156
Lepidopodinae :			
"Lepidopus xantusi"	(82)		—
Lepidopus caudatus	9	90–97	41+70–73=111–113
Assurger anzac	(*ca.* 120)		—
Tentoriceps cristatus	(*ca.* 120)		—
Evoxymetopon taeniatus	10	77	—
Eupleurogrammus intermedius	3	123–131	32–35+125–128=157–162
Eupleurogrammus muticus	3	143–147	41+150–151=191–192
Trichiurinae :			
Trichiurus lepturus	3	137	39–40+123–128=162–168
Lepturacanthus savala	4	111	32–35+124–130=159–162

Data for *Nesiarchus* (part), *Mimasea* & *Gempylus* taken from Matsubara & Iwai (1952) and Grey (1953) ; for "*Lepidopus xantusi*" from Jordan & McGregor (1899) ; for *Assurger anzac* from Alexander (1916) ; for *Tentoriceps cristatus* from Klunzinger (1884) ; for *Evoxymetopon taeniatus* from Gill (1863). Remainder original.

(5) Progressive reduction of the number of dorsal spines in the higher forms and their replacement by soft rays.

(6) Backward migration of the ventral fins. In the Gempylidae the pelvic girdle is embedded in the ligament between the cleithra, and the primitive position of the ventral fin-insertions in the Trichiuridae is likewise closely before or behind the level of the pectoral base. In *Benthodesmus simonyi* they are already further back than in *B. tenuis*, while among the Lepidopodinae the migration continues : an eye-diameter behind the pectoral base in *Lepidopus* and *Evoxymetopon*, an eye-diameter and a half in *Assurger* and finally five eye-diameters in *Eupleurogrammus*, but all the while a ligamentous connection between the pelvic girdle-rudiment and the symphysis is maintained. This situation has been discussed by Regan (1909 : 67).

(7) Hypertrophy of the dorsal musculature, with consequent elevation of the posterior confluence of the frontal ridges of the skull into a distinct sagittal crest (*Lepidopus*, *Trichiurus*) followed at a later stage by an adjacent elevation of the ethmo-frontal region continuing this crest forward along the snout (*Evoxymetopon*, *Assurger*, *Eupleurogrammus*, *Tentoriceps*).

(8) Increase in the number of pyloric caeca. In the Aphanopodinae, as in the

Gempylinae, the number lies within the range 6–9 (6–8 in 30 *Aphanopus* counted) ; in *Lepidopus* it is over 20 and may be much higher in *Trichiurus* (which needs to be studied from fresh material).

(9) Reduction of the soft anal fin from before backwards. In *Diplospinus* the soft anal extends nearly to the vent, so also in *Benthodesmus tenuis*. In *Aphanopus* and in *B. simonyi* the anterior rays are weak and probably of no functional consequence in the fin ; in *Lepidopus* and others only the last 20 rays or so form the true fin. In *Lepturacanthus* and in *Trichiurus* the whole fin is reduced to a series of minute spinules, while in *Eupleurogrammus* the fin as such has ceased to exist and only the basal and interhaemal elements remain, firmly interlocking with the haemal arches to form a continuous mid-ventral keel.

(10) Loss of the caudal fin and hypural bones, independently in *Trichiurus, Lepturacanthus, Eupleurogrammus* and *Tentoriceps*.

(11) Reduction in the extent of the intermuscular (pleural and epipleural) bones. In *Diplospinus* these long bones are a prominent feature in the skeleton and form a complete basket surrounding the abdominal cavity, but in all the other genera the space which they contain becomes a much smaller portion of the whole. In *Eupleurogrammus* a small " basket " supported by 14 rather smaller vertebrae is pushed to the anterior end of the trunk and is followed by 18–25 vertebrae without epipleurals.

Pari-passu with the major trends outlined above come sporadic tendencies, repeated at different levels :

(*a*) Excessive elongation of the body, a possible symptom of evolutionary inertia (*Benthodesmus, Assurger, Tentoriceps*).

(*b*) Hypertrophy of the second anal spine, with correlated condensation of the anterior basal and interhaemal elements into an enlarged supporting structure. (*Aphanopus, Lepturacanthus*).

(*c*) Reduction of the pelvic girdle and fins to an internal rudiment (*Aphanopus*) or their complete loss (*Trichiurus, Lepturacanthus*).

Classification of the Trichiuridae

The Aphanopodinae as now recognised comprise Gill's group (*Aphanopus*) with the addition of *Benthodesmus* and *Diplospinus*, genera recognized since Gill's time. They are forms in which the major changes from the Gempyline condition have been accomplished but in which the evolution of the Trichiurid caudal may still be seen proceeding. The discriminant characters of the primitive *Diplospinus* have already been noted ; it is a satisfactory ancestral form except possibly in the advanced barbing of the teeth, a character which, if not merely adaptive, may indicate an affinity with the ancestors of the Trichiurinae rather than with the *Nesiarchus-Aphanopus* line. *Aphanopus* is a secondarily specialized bathypelagic form having an enlarged postanal spine and associated endoskeleton. *Benthodesmus* is an attenuate type which has gone some way with *Aphanopus* (as evidenced by the endoskeleton of the anterior anal fin) and then stopped. *B. simonyi*, evidently derived from *B. tenuis*, shows several evolutionary trends in action in the same genus.

The Lepidopodinae are equivalent again to Gill's group (*Lepidopus, Evoxymetopon*) with the addition of *Eupleurogrammus* (removed from Gill's Lepturinae =

Trichiurinae) and of other genera subsequently recognised—*Assurger*, *Tentoriceps*, *Lepidopus* (as represented by *L. caudatus*) shows a great reduction in the spinous dorsal and the early stages in the uplift of the cranial crest and in the backward progress of the ventral fins; at the same time it has attained equilibrium in the development of vertebrae and soft fin-rays, and is well on the way towards losing its anal fin. The so-called "*Lepidopus xantusi*" of unhappy memory is inadequately known, but would appear to be more primitive than *L. caudatus* and may even deserve generic status in a position between *Lepidopus* and *Diplospinus* in the main stem. In my opinion *L. caudatus* represents the termination of a very old line and its close similarity of skull to *Trichiurus* is the result of parallelism and not of any closer relationship. The remaining Lepidopodine genera—*Evoxymetopon*, *Assurger*, *Tentoriceps*, *Eupleurogrammus*—have in common an elevation of the ethmo-frontal region to continue the sagittal crest forward from the nape to the snout; in *Eupleurogrammus*, the only one of this quartet which I have been able to handle, the homologies in relation to *Lepidopus* are easily discernible and, together with published figures, give sufficient indication of the likely condition in the other three. *Evoxymetopon* is probably the most primitive of this group, in its shorter body and lower median fin-ray counts and in the position of the ventrals and presence of a caudal fin, but has a rather steep profile. The ecaudate and highly perfected *Eupleurogrammus* may have been descended from this line, sharing with the Lepidopodines (and not with *Trichiurus*, with which it was formerly classified) the uniseriate palatine teeth, median lateral line, ethmo-frontal elevation, ventral fins and rounded operculum. The elongate, caudate *Assurger* and the ecaudate *Tentoriceps* form another like pair.

The Trichiurinae are now restricted to *Trichiurus* and *Lepturacanthus*, the latter Fowler's sub-genus upgraded to full generic rank. They are unique among the Trichiuridae, not for their loss of a tail (which has occurred elsewhere and independently), but in having a band of villiform teeth on each palatine rather than a single series, in having lost the last vestige of a pelvic girdle and fins and in having a low-descending lateral line. Other differences assume greater significance in relation to these. It is therefore likely that the fundamental cleavage between the Trichiurinae and the other two sub-families goes deeper than has previously been supposed.

It is interesting to observe, in conclusion, that although there has been such a great reduction in the number of nominal species formerly placed in *Trichiurus* the residue are now distributed through five genera—*Lepidopus*, *Trichiurus*, *Lepturacanthus*, *Eupleurogrammus* and *Tentoriceps*.

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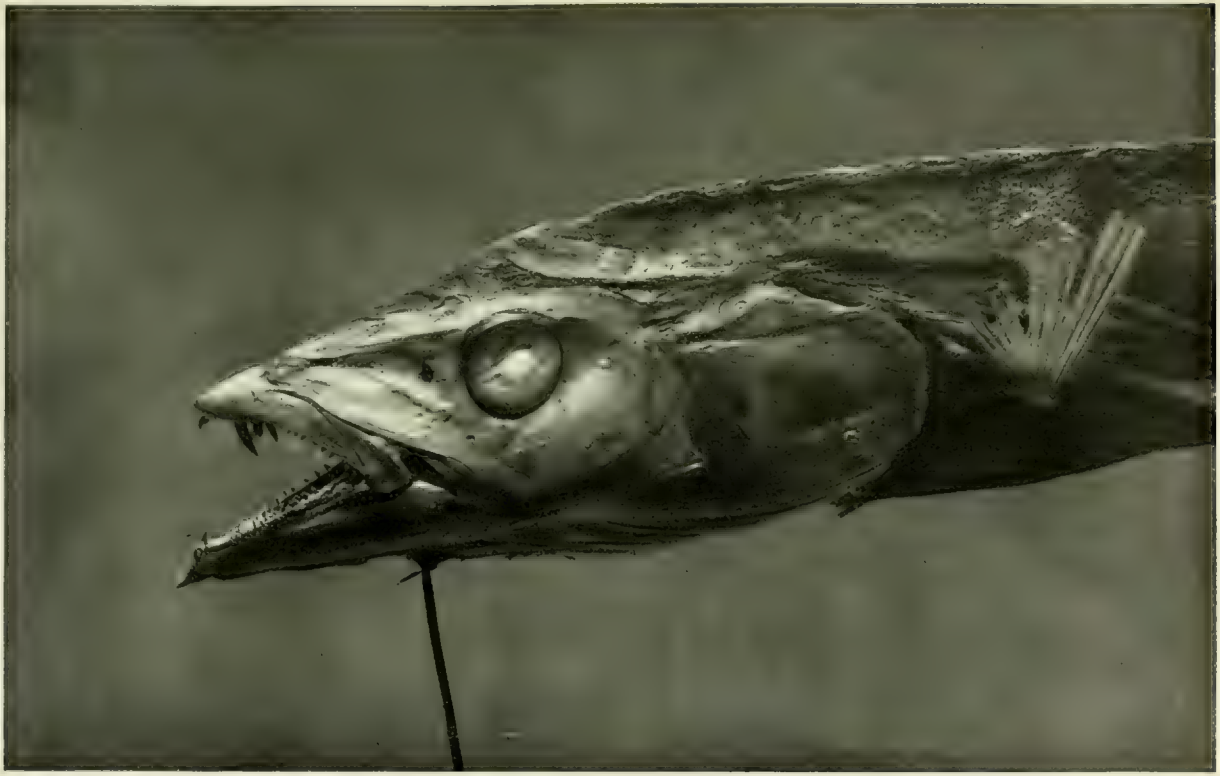

Assurger anzac (Alexander). Head of Holotype, 1,415 mm. T.L. (Photograph by courtesy of Dr. L. Glauert, Director of the West Australian Museum, Perth.)

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NATURAL HISTORY

VARIATION, RELATIONSHIPS AND EVOLUTION IN THE *PACHYCEPHALA PECTORALIS* SUPERSPECIES

(*AVES, MUSCICAPIDAE*)

IAN C. J. GALBRAITH

BULLETIN OF
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ZOOLOGY Vol. 4 No. 4
LONDON : 1956

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PRESENTED
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BY

IAN C. J. GALBRAITH

BRITISH MUSEUM NATURAL HISTORY

Pp. 131–222 ; 8 Text-figures.

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VARIATION, RELATIONSHIPS AND EVOLUTION IN THE *PACHYCEPHALA PECTORALIS* SUPERSPECIES (AVES, MUSCICAPIDAE)

By IAN C. J. GALBRAITH

SYNOPSIS

The Australasian species *Pachycephala pectoralis* is remarkable for the great number and variety of geographical representatives which, since they intergrade, must be included in it. Although cited in recent evolutionary literature (Meise 1936, Dobzhansky 1937, Mayr 1942, Ripley 1945, Cain 1954*a*), the species has not previously been revised as a whole. It presents a wealth of geographically-variable plumage characters, whose relative systematic importance can be assessed from their co-variation. The complicated character-geography of the *P. pectoralis* superspecies is here interpreted in terms of colonizations by two major stocks, followed by divergence in isolation, great expansions of range, and extensive secondary intergradation. Whether two forms, on meeting, will interbreed or coexist as distinct species, seems to depend less on their degree of relationship than on internal and external ecological factors.

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INTRODUCTION

Pachycephala pectoralis, the Golden Whistler, is probably unique in the richness of its geographical variation. More than seventy subspecies can be recognized, extending from Java and the Moluccas to Tasmania and Tonga. Many of these are so unlike that they would certainly be considered as distinct species, were it not for the more or less complete intergradation between them.

There has been no comprehensive checklist of the species since that proposed by Mathews (1930), in which forms now generally recognized as subspecies of *P. pectoralis* are separated into eleven species. But as early as 1908 Rothschild and Hartert had suggested that the distinctive races of the Solomons are conspecific with more characteristic *P. pectoralis*, and this was confirmed twenty years later (Hartert, 1929) by the discovery of hybrid populations. Rensch (1931) included the Sumban race and its relatives, but not those of the northern Moluccas. Mayr (1932*a*, *b*) placed even the aberrant forms of northern Fiji in *P. pectoralis*, because they are connected with that species by intermediate forms. The conspecificity of diverse forms has been accepted in subsequent lists (van Bemmel, 1948 ; Mayr, 1941*a*, 1945, 1954*a*, 1955), which together cover almost the whole range of the species. All these forms are accepted here as belonging to *P. pectoralis*.

P. soror in the hill forest of New Guinea is very like nearby races of *P. pectoralis*. Over most of its range it replaces this species ; but a race of *P. pectoralis* lives so close to populations of *P. soror* (Rand, 1940) that the barriers between them are probably intrinsic (p. 166). Thus two very similar forms seem to be genetically sympatric (Cain, 1953), and must be considered as distinct species ; while others which differ much more, and seem to be actually less closely related, intergrade and must be considered conspecific. This situation is not unknown in other animals (e.g. *Acanthiza*, Mayr, 1942, 174), but the striking example in *Pachycephala* has been pointed out only by Cain (1954*a*) as a result of the present review.

Scope and presentation

Four species are considered, which form a single superspecies with a triplet (see p. 172) in New Guinea:

P. schlegelii Schlegel, New Guinea mountain forest from 4,000 or 5,000 to 12,000 ft.
P. soror Sclater, New Guinea hill forest from 2,200 to 5,200 ft.
P. pectoralis (Latham), Lesser Sunda Isles and Moluccas to Tasmania and Tonga; but absent from New Guinea except for the south-east coast, and disturbed habitats in the Snow Mountains between 5,200 and 8,000 ft.
P. flavifrons (Peale), Samoa.

No linear arrangement can be satisfactory, since *P. pectoralis* connects the other three species.

Text-figure 6 (end-fold) gives the ranges of the species and subspecies, and of the subspecies-groups of *P. pectoralis*. The latter seem to be natural groups, though because of gene-interchange their boundaries are not sharp and have to be shown rather arbitrarily (see Text-fig. 8):

Lesser Sundan subspecies-group A (subspecies 1–5).
Moluccan subspecies-group B (subspecies 6–8).
Solomons subspecies-group C (subspecies 9–17).
Fijian subspecies-group D (subspecies 18–21).
Northern Australian subspecies-group E (subspecies 22–27).
Southern Australian subspecies-group F (subspecies 28–33).
Southern Melanesian subspecies-group G (subspecies 34–38).
Widespread subspecies-group H (subspecies 39–57).

P. schlegelii and *P. soror* have three subspecies each, while *P. flavifrons* is monotypic. Many forms recognized as distinct subspecies by recent authors have been combined in this presentation (see p. 175), although a number of these are distinct enough to be separated according to current usage (list on p. 205).

The use of subspecies names is not helpful to the reader unless he is already familiar with the group under discussion. Nor is it usually necessary, since most subspecies are easily characterized by their geographical ranges (cf. Wilson & Browne, 1953). In this paper the range citation, given in a condensed and approximate form, is followed by a cipher for direct reference to the map (Text-fig. 6). This cipher consists of the number of the subspecies within its species, preceded by the subspecies-group letter for subspecies of *P. pectoralis*. Where infrasubspecific variation is discussed, parts of the subspecies range are indicated by lower-case suffixes. Thus "Sumbawa to Alor A3" indicates the form of *P. pectoralis* on Sumbawa, Flores, Lomblen, Pantar and Alor (which from "Lomblen to Alor A3b" is slightly larger and larger-billed). The exact range of any form can be found from the check-list (p. 195), which is lettered and numbered to correspond.

Subspecies names are useful in referring to forms whose geographical ranges are diffuse or difficult to define: " *dahli* E25 " is used for the subspecies of *P. pectoralis* which ranges from south-eastern New Guinea and Fergusson Island to many small islands in the Bismarck Archipelago. The range of *dahli* is shown inset on the map.

Material

I have seen at least one adult male and one adult female of every subspecies recognized by recent authors, except for the following: no specimens of H46 and H50; no adult male of D21; no adult female of C15, G37a & b, H49, H52 and H56 (juveniles seen) and E25c (female unknown). I have examined the following types in the British Museum (Natural History): *fulvotincta* Wallace A3a, *mentalis* Wallace B6, *neglecta* Layard (= D18b), *aurantiiventris* Seebohm D19a, *torquata* Layard D20a, *fuliginosa* Vigors & Horsfield F28b, *fusca* Vigors & Horsfield (= F30b), *variegata* Gray (= G34), *cucullata* Gray G36, *chlorurus* Gray G37a, *intacta* Sharpe G37d, *fuscoflava* Sclater H42, *xanthocnemis* Gray (= H43b), *clio* Wallace H45, *collaris* Ramsay H47a, *vitiensis* Gray H55, *klossi* Ogilvie-Grant and *bartoni* Ogilvie-Grant (*P. soror* 2 & 3).

Unfortunately, many of the available series were very short, and the measurement tables compiled (p. 212) are inadequate for proper statistical treatment. Individual variation and fine geographical variation are therefore not considered in this paper. Where the available material was inadequate full use has been made of published descriptions and measurements, especially those of Mayr (1932*a*, *b*, and 1954*a*).

I have studied *P. pectoralis* in the field on Guadalcanal C11 and San Cristobal C17a, and seen and heard it near Sydney F30b, on Lord Howe and Norfolk Islands F32 & 33, and on Efate and Santo G37b & d. I have also studied *P. implicata* (which is rather closely related to the *pectoralis* superspecies) in the mountains of Guadalcanal (Cain & Galbraith, 1956).

PLUMAGE PATTERNS

Pigments

All the colours in the various plumages of the superspecies are produced by combinations of yellow, black and brownish pigments (Table I). The yellow pigment is soluble in boiling alcohol or pyridine, and turns a transient blue-green with concentrated sulphuric acid. It is therefore a carotenoid (Cain, 1950, 104). Carotenoid

TABLE I.—*Composition of Plumage Colours.*

	Carotenoid.			
Melanins.	None.	V. pale.	Pale.	Deep.
None	White	Pale yellow	Lemon-yellow	Golden- to orange-yellow
Eumelanin:				
Barbs clear, barbules saturated	Grey	Olive-grey	Olive-green	Golden-olive
Granules in barbs, barbules saturated	Dull black	—	Olive-black	—
Saturated	Black	—	—	—
Phaeomelanins:				
Pale	Sandy to dull pink	Cream	Cinnamon to vinous	Citrine
Deep	Brown to rufous	Russet	Tawny-orange	—

tends to be more concentrated in the barbs than in the barbules of the feather. The other pigments, if not saturated in both elements of the vane, are more concentrated in the barbules than in the barbs. They are granular. Under the microscope black granules still appear intense black, while brown ones vary considerably in hue and intensity. The black and brown pigments are presumably eumelanins and phaeomelanins. Parts of the vane devoid of melanins are filled with minute bubbles, which by multiple internal reflection add to the brilliance of the whites and yellows. Most contour feathers are grey basally, with the black granules forming bands across the barbules.

Patterns

It is convenient to describe the variation of the male pattern throughout the superspecies in terms of departure from a standard. The descriptions will be briefest, and the peculiarites of the various forms most clearly apparent, if the pattern chosen as standard combines all the variants which are more common than their alternatives. This condition is fulfilled by the pattern of males of *P. pectoralis* in the Bismarcks H48–51, which is shown diagrammatically in Text-fig. 1 (top), and described below.

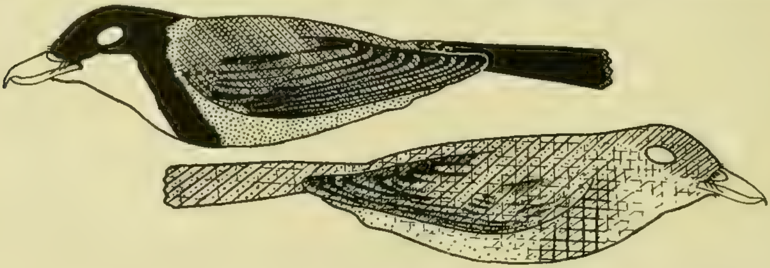

Fig. 1.—Diagram of the standard plumage patterns for the superspecies. Male (above, facing left) H48–51 ; female (below, facing right) H52. Not to scale. Colour key : diagonal hatching, grey (without stipple) or olive (with stipple) ; cross-hatching, brown and rufous hues ; stipple, yellow ; black, black ; white, white. The same conventions are used in all the diagrams of plumage pattern (Text-figs. 1–3 and 5).

Adult male. White chin and throat separated by black gorget, between auriculars, from golden-yellow underparts; fore-edge of gorget formed by black tips of white feathers, hind-edge by black feathers overlying yellow ; black cap and auriculars separated by yellow collar across hind-neck from golden-olive mantle ; wings dull black with olive outer edges to all feathers, fading to grey towards tips of outer primaries ; inner edges of quills whitish ; tail and upper tail-coverts black with olive tips, and olivaceous traces at bases of outer quills.

It is harder to select a standard for the female plumage, since the patterns are much vaguer than those of the males, and the variation is more quantitative than qualitative. The following description and the diagram (Text-fig. 1, bottom) best fit some females of the widespread group H, and especially those from Ndeni H52.

Adult female. Throat pale buff with faint dark fringes at sides ; gorget brownish, vaguely defined, grading into brownish wash on breast and flanks ; mid-belly and under tail-coverts free from melanins ; under tail-coverts pale yellow, breast and belly washed with yellow ; upper parts citrine ; collar, rump and tail brighter ; cap greyer than mantle, auriculars cinnamon ; wings blackish-brown with citrine outer edges to all feathers, fading to greyish towards tips of outer primaries ; inner edges of quills whitish.

Retarded and juvenile plumages

Males are sometimes found in plumage like that of the adult females (" II Phase " of Mayr, 1932*a*, *b*), though commonly with more intense carotenoid. They agree with adults in tail shape and in having black bills, and their testes are often enlarged (Baker, Marshall & Harrison, 1940). They are evidently adult males in a " retarded " plumage (Mayr, 1933) : in Victoria and Tasmania at least they are known to breed in this condition (Chandler, 1912 ; Howe, 1927 ; Lawrence, 1952).

Juveniles of both sexes have brown or straw-coloured bills, and softer wings and more pointed tail-feathers than adults. In pattern they resemble adult females, except that they have the edges of the wing feathers rufous, the cap olivaceous, the mantle often browner and the carotenoid pigment more dilute (I Phase). Nestlings are commonly rufous all over ; but in the lesser Sunda Isles (nestling of A3b seen) are greyish with darker shaft-streaks beneath. Only Mayr (1932*a*, *b*) has systematically described immature plumages, and I have not examined sufficient immature skins from parts of the range not treated by him to attempt a survey of their variation.

At first sight the female and juvenile patterns seem very different from that of the adult male. But the distribution of pigments is much the same—except that carotenoids are greatly diluted, there are no solid blacks, and eumelanins are more or less replaced by phaeomelanins. As a result, these patterns are less sharply defined and stereotyped than that of the male, and show a greater range of colours.

Visual significance

In many birds the upperparts are cryptic, while the underparts bear a conspicuous pattern which plays a part in intraspecific display. The standard male pattern of *P. pectoralis* is a good example of this. Both the ventral and the dorsal pattern embody transverse bands which contrast strongly with the ground-colour (see Cott, 1940). The bright underparts contrast with the forest background, so that the black gorget (exploiting maximal tone-contrast against the white, and an especially effective colour-contrast against the yellow) is an emphatic feature. The olive upperparts, on the other hand, conform with the background, and the yellow collar is disruptive in effect. Females and juveniles tend to be inconspicuously coloured, with neither emphatic nor markedly disruptive features.

This common species has been largely neglected by Australian ornithologists (except Lawrence, 1952), and nothing seems to be known of the part played in intraspecific display by the conspicuous male ventral pattern. Although we saw neither courtship nor aggressive displays in the Solomons, the general behaviour of these birds (Cain and Galbraith, 1956) is much what might be expected from a study of their colour-patterns. The males show themselves freely to a ground observer as they move about below the canopy, whistling loudly. But although they will sing from bare branches overhung by foliage, they avoid all perches exposed to the sky.

Females of *P. pectoralis* on Guadalcanal C11, like those of many other subspecies, are dull in colour. They are very silent and skulking, seldom seen as they move about in dense thickets near the ground. Those on San Cristobal C17 are as bright yellow beneath as the males, but lack the black gorget. They are often seen in company with the males in the upper substage, usually silent, but occasionally heard to give alarm calls and quiet whistles. A related species in the mountains of Guadalcanal (*P. implicata*) has the females actually more conspicuous than the males. They are not more retiring than the males, and are more vocal than the females of *P. pectoralis*. The males of *P. implicata* are inconspicuously coloured in olive and blackish, and are much more silent and retiring than those of *P. pectoralis*. On the other hand, a pair of this species was seen feeding exposed in the tops of small trees: perhaps the direction of predation is less important to these more uniformly-coloured birds.

VARIATION

Geographical variation in the superspecies is conspicuous and complex. Marked sexual dimorphism is normal, but in three widely-separated races of *P. pectoralis* the males are permanently hen-feathered, while *P. flavifrons* has cock-feathered females. The sporadic occurrence, in sexually dimorphic forms, of breeding males in female plumage shows that hen-feathering is not very important here, either as an indicator of genetical change or as a potential barrier to interbreeding.

The bold pattern of the male is subject to striking variation. For example, in some forms the throat is yellow instead of white, and some of these lack the black gorget. These differences are not unifactorial, since for almost every pair of contrasted characters intermediate states are to be found. Single characters cannot be used to delimit natural groups, since not one variant is confined to a single subspecies-group of *P. pectoralis* (as distinguished by the whole constellation of characters of both sexes) and shown by every race belonging to that group. Most are both polyphyletic in origin and labile within groups. The marked geographical variation of the female pattern does not present the same appearance of discontinuity, and there is less temptation to erect a classification based on single characters of the females.

Size variation

The largest subspecies of *P. pectoralis* have wings over 30% longer than the smallest. If their proportions are the same, they should therefore be more than twice as heavy. Unfortunately, weight measurements are available for very few forms in the superspecies, so that wing lengths are for the present the best indication of body size. Certain subspecies which are evidently very closely related differ markedly in size, which is therefore not generally of much importance in assessing relationships ; but some of the discontinuities between subspecies-groups are marked by sharp changes in size as well as in other characters. A coarse grading into size-classes adequately expresses the major variation, which more detailed treatment would tend to obscure. In any case, too few specimens of many forms were available for quantitative treatment to be satisfactory. Snow (1954) has pointed out that quantitative differences (in size, proportions, intensity of pigmentation, etc.) are often adaptive, and cannot be used as clues to relationships and past history until their present environmental relations have been worked out. Conversely, where the past history has been as complex as in the *pectoralis* superspecies, such differences cannot be shown to be adaptive until relationships have been established (by studying the co-variation of more stable characters). Two forms on neighbouring islands might differ in size, not because the climates were different but because they were the same, if the forms belonged to different subspecies-groups whose size/temperature relationships (Snow, 1954, 22) had been evolved under different climates.

The various forms are graded into five classes on the average wing lengths of adult males. But the arbitrarily-selected limits of these classes have in a few cases been relaxed, to avoid separating closely-related forms whose small difference in size happens to transgress them. The southernmost Australian forms are classed as " large ", not as " very large ", because the appearance of the skins (prepared by many different collectors) strongly suggests that they are considerably smaller birds, though with relatively long wings (perhaps in relation to their nomadic habit) than the " very large " ones of the Solomons and elsewhere. This can only be decided when weight measurements are available. The middle class, containing the most forms, is of wing lengths from 90 to 95 mm.; those from 80 to 85 mm. are graded as " very small", from 85 to 90 as " small ", from 95 to 100 as " large " and over 100 as " very large ". The following forms fall outside the middle class :

VERY SMALL BIRDS. Sumba, Java to Alor, and Flores Sea and Salayer A1–5 ; midwestern Australia E22 a–c (size increasing north-eastwards).

SMALL BIRDS. Rennell and San Cristobal C16–17 ; northern Australia to southern New Guinea E22d–24 ; New Caledonia, New Hebrides and Vanikoro G34 & 36–38 ; Timor to Damar H39–41 ; Sula and Peleng Isles H45–46 ; large islands in the Bismarcks H48 ; Kandavu H54 ; *P. soror* ; *P. schlegelii* ; *P. flavifrons*.

LARGE BIRDS. Ternate, Tidore and Obi B7–8 ; Vella Lavella to Gatukai C13 & 15 ; Tasmania and southern Australia F28–30, size decreasing northwards ; Tabar H50 ; Lau archipelago H56.

VERY LARGE BIRDS. Bougainville to Malaita, and Rendova and Tetipari C9–12 & 14 ; Loyalty Isles G35 ; Tenimber Isles H42 ; Lihir H49 ; Tonga H57.

Differences in bill size are even more marked, with the largest bills some 60% longer than the smallest, and the bill may be stubby, stout or slender. However, closely related forms differ in bill size even more than in wing length, and the accuracy of this measurement is not sufficient for the forms to be graded with any degree of certainty from the scanty data available. Tail and tarsus lengths are only comparable when expressed as relative lengths, which vary between individuals much more than the absolute measurements. Therefore none of these measurements is dealt with comprehensively, though there is some discussion of climatic correlation in certain parts of the range (p. 186).

Male character-geography

Some of the most conspicuous variations appear to be qualitative and discontinuous, but hybrid forms often show intermediate states. Probably most of the variations are in fact potentially continuous—but it is convenient to deal with the geographical distribution of the more important variations in terms of discontinuous "characters", at the same time mentioning the occurrence of intermediate conditions.

(1) Hen-feathered. Rennell C16, Norfolk Island F33 (sexes almost indistinguishable); Salayar A5 (male in a female type of plumage, but more advanced in character than its own female).

The hen-feathered races were considered as separate species until Mayr (1932*a*, 5) pointed out the relative unimportance of the character. Since individual males of dimorphic subspecies can breed in female plumage, hen-feathering involves neither a radical change in the genome nor complete breakdown of courtship and territorial displays. Variations of the male pattern such as " no gorget ", " no collar ", " cap pale " and " tail pale " may be considered as partial hen-feathering, and the San Cristobal form C17 especially shows several such indications.

The three fully hen-feathered forms are not considered further in the male character-geography.

(2) Chin black. Sumba A1; Morotai to Batjan B6–7; Solomons except San Cristobal C9–15; *P. schlegelii*, *P. flavifrons*.

(3) Throat and chin black. Tonga H57.

In *P. flavifrons* there is much black at the base of the throat feathers, which shows as irregular barring. Another approach to the black-throated condition is shown in the reduction of the throat patch on Sumba A1 (where black malar feathers intervene between it and the auriculars), from Java to Alor A2–3, and in *P. soror* and *P. schlegelii*.

(4) Throat yellow. Solomons C9–17 (variable in hybrids on small islands off Shortland E26); northern and central Fiji D18–21; Tenimber Isles H42; *P. flavifrons* (individually variable).

Juveniles on Vanikoro G38 have yellow throats, and there is a tendency for the throats of juveniles in the New Hebrides G37 and on Utupua H53 to be yellowish (Mayr, 1932*b*). A few yellow feathers occasionally appear in the white throats of adult males. I have seen these in males of *P. pectoralis* from Teste Island E25b, Lord Howe Island F32, New Caledonia G34, Loyalty Islands G35, Aneitum G36 and Kandavu H54, and in *P. soror* from the Snow Mountains 2a. But they seem to occur most frequently in *P. schlegelii*—in eight of thirty-one adult males examined.

(5) Bases of throat-feathers white. Obi B8; Solomons C9–17; northern and central Fiji D18–21; midwestern Australia to small islands in the Bismarcks, and hybrids off Shortland E22–26; Vanikoro G38; Tenimber Isles H42; Sula and Peleng Isles H45–46; Louisiades H47; Ndeni, Santa Cruz islets and Utupua H52–53.

(6) No gorget. Malaita C12; Viti Levu and Vanua Levu D18a and 19a; *P. flavifrons*.

The gorget is more or less broadly interrupted in individual males on the islands between Koro and Taviuni on the one hand, and Viti Levu and Vanua Levu on the other—D18b, 19b & c.

(7) FORE-EDGE OF GORGET DEFINED BY PALE FEATHERS. Sumba and Java to Alor A1–3; northern Moluccas B6–8; Solomons except San Cristobal (and the gorgetless forms on Malaita and Rennell) C9–11 & 13–15; Ceram H43; Ndeni and Santa Cruz islets H52; *P. schlegelii.*

In these forms the black of the gorget deeply undercuts the white or yellow of the throat, whereas in the standard pattern the edge of the gorget is defined on the underlying layers of feathers at about the same level. On San Cristobal C17, in the hybrids on the outliers of Shortland E26, and on Buru H44, the gorget undercuts the throat-patch, but there are also some black tips.

(8) GORGET CUT OFF FROM AURICULARS. Northern Moluccas B6–8; New Caledonia G34; Ceram H43; Ndeni and Santa Cruz islets H52.

In all these forms the throat-feathers are unusually long, extending further back than the auriculars. They are best developed from Morotai to Batjan B6–7 (where they cover most of the gorget), and least so on New Caledonia G34 (where only the lateral feathers are appreciably lengthened). In B6–7 and G34 the gorget is itself reduced, and does not join the auriculars even beneath the white feathers. On Vella Lavella and Ganonga C13 the yellow feathers extend behind the auriculars, but the gorget is too broad to be cut off.

(9) GORGET VERY BROAD. Vella Lavella and Ganonga C13; *P. schlegelii.*

(10) GORGET VERY NARROW. New Caledonia G34; Kandavu H54; *P. soror.*

(11) BREAST RUFOUS. Sumba A1 (intense, extending to flanks and belly), Java A2a (less intense, especially on belly), Bali A2b (still less intense on flanks and belly), Sumbawa to Alor A3 (confined to band behind gorget), islands in Flores Sea A4 (very faint, barely detectable on belly and flanks); Santa Anna C17b and individuals on San Cristobal C17a (patch behind gorget); New Caledonia G34 (patch behind gorget); *P. schlegelii* (extending to flanks and belly; very intense from Snow Mountains to south-eastern New Guinea 3, somewhat less so in Vogelkop and Cyclops Mountains 1 & 2).

There is a rufous wash centred on the vent on Taviuni, Koro and Vatu vara D20–21, Ceram H43, Ngau H55, and in individuals on Aneitum G36.

Where very pale rufous phaeomelanin combines with pale yellow carotenoid (as in the Flores Sea A4), the tawny-orange produced is rather like the orange-yellow of very intense carotenoid (as on Vanua Levu D19). The difference is easily seen through the microscope, since the phaeomelanin appears granular.

(12) CAROTENOID VERY DEEP (ORANGE-YELLOW). Vella Lavella and Ganonga C13; Vanua Levu to Koro and Vatu vara D19–21; Louisiades H47; Lihir H49; Manus H51.

(13) CAROTENOID PALE (LEMON-YELLOW AND GREENISH-OLIVE). Mid- and north-western Australia E22, deepening northwards E22a to 23; Tasmania and southern Australia F28–30, deepening northwards F29 to 31; New Caledonia, New Hebrides and Vanikoro G34 & 36–38; Babar H40; Utupua H53; *P. soror.*

(14) FOREHEAD YELLOW. Viti Levu, Vanua Levu and Vatu vara D18a, 19a & b & 21 (sometimes a few yellow feathers on Ovalau, Rambi and Kio D18b & 19c); *P. flavifrons* (sometimes white, in white-throated individuals).

(15) CAP PALE. Santa Anna C17b (olive, with blackish lores and auriculars) and

San Cristobal C17a (variable, from olive to black); New Caledonia G34 (grey); Aneitum G36 (dull black with more or less olive scalloping).

(16) NO COLLAR. Vella Lavella and Ganonga C13, Ndeni and Santa Cruz islets H52, *P. flavifrons* (melanic forms with no trace of a collar); Fiji, except for Vatu vara and Kandavu, D18–20, H55–56 (black of cap extends far down on hind-neck, followed by a yellowish trace); Malaita C12, New Caledonia G34, *P. soror* (yellowish trace); San Cristobal C17 (yellowish trace on hind-neck, clear yellow patches at sides of neck).

The collar is very vague and narrow on the islands in the Flores Sea A4, from Kulambangra to Gatukai C15 and on the Tenimber Islands H42. It is narrow and washed with olive on the nape on Sumba and from Java to Alor A1–3, on Rendova and Tetipari C14, in mid- and north-western Australia E22, in Tasmania, southern and eastern Australia and on Lord Howe F28–32, from the Loyalty Isles to Vanikoro G35–38, on Timor H39a, the Louisiades H47, Utupua H53 and Kandavu H54.

(17) MANTLE BLACK. Vella Lavella and Ganonga C13, Ndeni and Santa Cruz islets H52, *P. flavifrons* (wholly black); islands in Flores Sea A4, Rendova and Tetipari C14, Taviuni and Koro D20, Ngau and Lau archipelago H55–56 (feathers black-centred, individually variable from olive with concealed black spots to black with olive scalloping).

(18) WING BLACK. Islands in Flores Sea A4; Vella Lavella, Ganonga, Rendova and Tetipari C13–14; *P. flavifrons*; *P. schlegelii*.

In these forms the pale edges to the wing-feathers are absent or exceedingly narrow. The pale edges are narrow, and the primary-coverts entirely black, on Taviuni, Koro and Vatu vara D20–21, in *dahli* E25, on Ceram and Buru H43–44, Ndeni and Santa Cruz islets H52 and Ngau and the Lau archipelago H55–56.

(19) OLIVE VERY DARK. Kulambangra to Gatukai C15; Fiji D18–21 & H54–56; Ceram and Buru H43–44; *P. soror*; *P. schlegelii*.

Normally the bases of the barbules, as well as the barbs, are yellow, giving a more or less pronounced herring-bone pattern under the microscope. In the above forms the barbules are black down to their junctions with the barbs.

(20) OLIVE TINGED WITH BROWNISH. San Cristobal C17; Koro and Taviuni D20; Ceram H43; Louisiades H47; individuals on Aneitum G36.

The phaeomelanic wash is deepest on tail, upper tail-coverts, rump and secondaries.

(21) WING QUILLS GREY-EDGED. Midwestern Australia to small islands in the Bismarcks E22–25; Tasmania F29; Damar H41; *P. soror* in Snow Mountains 2a.

The wings are unusually grey in southern Australia F28 & 30, becoming more olive northwards; and in eastern Fiji D19 & 21 & H56, becoming more olive westwards (towards Viti Levu and Kandavu D18 & H54). They are also unusually grey in all populations of *P. soror*. They are variable in colour in the hybrids on outliers of Shortland E26.

(22) UPPER WING-COVERTS YELLOW-EDGED. Viti Levu and Vanua Levu D18–19; midwestern Australia to small islands in the Bismarcks E22–25; Tasmania, southern and eastern Australia and Lord Howe F28–32; Loyalty Islands G35.

The upper wing-coverts are edged with yellower olive than the mantle in many forms; those listed above show this most conspicuously.

(23) UPPER TAIL-COVERTS ALL-OLIVE. Kulambangra to Gatukai C15; San Cristobal C17; northern Fiji, except Koro and Vatu vara, D18–20a; mid- and north-western Australia E22; Tasmania, southern and eastern Australia and Lord Howe F28–32; New Caledonia to Banks Islands G34–37; Timor H39; Tenimber Isles H42; Louisiades H47; Kandavu H54; Tonga H57; *P. soror.*

(24) TAIL PALE. Tasmania F29, New Caledonia, Loyalty Islands and Aneitum G34–36, Timor H39, western Louisiades H47a (no solid black); San Cristobal C17 (more or less black); south-western and South Australia F28, New Hebrides from Erromango northwards G37, Misima H47b, Kandavu H54, *P. soror* except the Snow Mountains 1 & 3 (black subterminal patch); south-eastern Australia and Lord Howe F30 & 32, Babar H40, Rossel H47c (more than half black); mid-western Australia E22a–c, southern Queensland F31a, Damar H41, *P. soror* in Snow Mountains 2 (wide olive edges basally); north-western Australia E22d, northern Queensland F31b (narrow olive edges basally).

The pale part of the tail, usually olive, is grey from south-western Australia to Tasmania and Victoria F28–30a, and sometimes greyish in northern Queensland F31b.

(25) UPPER TAIL-COVERTS ALL-BLACK. Sumba, Java to Alor, and islands in Flores Sea A1–4; Morotai to Obi B6–8; Vella Lavella and Ganonga C13; Ceram, Sula and Peleng Islands H43 & 45–46; Ndeni and Santa Cruz islets H52; *P. schlegelii*; *P. flavifrons.*

Even in these forms, the shortest coverts usually have narrow olive tips. Males on Buru H44, and from some other localities, have the tips of all the coverts extremely narrow.

(26) TAIL ALL-BLACK. Sumba A1; Morotai to Batjan B6–7; Vella Lavella and Ganonga C13; Ndeni and Santa Cruz islets H52; *P. schlegelii*; *P. flavifrons.*

There are sometimes narrow and obscure olivaceous tips to the lateral tail feathers, even in these forms. The tips are unusually narrow from Java to Alor A2–3, on Obi B8, in most of the Solomons C9–12 & 14–15, and from Ceram to Peleng H43–46.

Female character-geography

(1) COCK-FEATHERED. *P. flavifrons* (throat and forehead patterns less sharply defined than in the male).

Certain single characters of the female (such as a white throat, a sharply defined gorget, bright yellow underparts, a pure grey cap and pure olive mantle, and a partly black tail) tend perhaps towards the male pattern. Often they appear independently, but on San Cristobal C17, and also in northern members of group E and in *P. soror*, most of the characters mentioned occur together—these forms have an advanced type of female plumage. Individual females of the race on Vella Lavella C13a (whose males are all-black above) have black gorgets (Mayr, 1932*a*, 17). A partly cock-feathered female from Malaita C12 is reported by Mayr (1932*a*, 21). I have seen several specimens which (though sexed as females) are partly or wholly in the plumage of the adult male, but consider it unwise to rely on the sexing of these, since they carry no indication that the collector had noticed the discrepancy between gonads and plumage.

P. flavifrons is not considered further in the female character-geography.

(2) BILL PALE. Solomons C9–17 (palest from Guadalcanal to Kulambangra and on Rennell C10c–11 & 15–16, darkest on Malaita, Vella Lavella and Ganonga C12 & 13); Rambi and Kio D19c.

(3) THROAT WITHOUT MELANIC WASH. Islands in Flores Sea and Salayer A4–5, midwestern Australia E22a–c, New Caledonia to Banks Islands G34–37, Timor and Babar H39–40, Louisiades H47, Utupua H53, *P. soror* (wholly white); north-western Australia to small islands in the Bismarcks, hybrids near Shortland and the Snow Mountains E22d–27, Vanikoro G38, *P. schlegelii* in the Vogelkop and Cyclops Mountains 1 & 2 (white, more or less mottled); San Cristobal C17 (pure yellow).

(4) THROAT YELLOW. Choiseul to Russel Isles, central Solomons, Rennell and San Cristobal C10 & 13–17; Tenimber Isles H42.

(5) CHEEKS YELLOWER THAN THROAT. Bougainville, Guadalcanal and Malaita C9, 11 & 12; Viti Levu and Vanua Levu D18a & 19a.

(6) THROAT BARRED. Morotai to Obi B6–8; Bougainville, Guadalcanal and Malaita C9, 11 & 12; Viti Levu and Vanua Levu D18a & 19a, and individuals on Ovalau, Rambi and Kio D18b, 19b–c; north-western Australia to small islands in the Bismarcks, hybrids near Shortland, and the Snow Mountains E22d–27; Tasmania, southern and eastern Australia, Lord Howe and Norfolk Islands F28–33; Damar H41; Sula and Peleng Islands H45–46; Tonga H57; *P. schlegelii* (faintly in the Vogelkop 1).

There is no sharp distinction between subterminal barring and terminal fringing of the feathers. There is a tendency towards heavy fringing, not entirely confined to the sides of the throat, from New Caledonia to the Banks Islands G34–37, in the Louisiades and Bismarcks H47–48, and on Utupua H53.

(7) THROAT AND BREAST SHAFT-STREAKED. *P.p. dahli*, hybrids near Shortland, and Snow Mountains E25–27; Vanikoro G38; Manus H51.

(8) UNDERPARTS SHAFT-STREAKED. Solomons except San Cristobal C9–16; Viti Levu and Vanua Levu D18a & 19a, and individuals on Ovalau, Rambi and Kio D18b & 19b–c.

(9) GORGET EUMELANIC. Morotai to Batjan B6–7, *P. schlegelii* east of the Vogelkop 2–3 (pure grey); Choiseul and Kulambangra to Florida, Rennell and San Cristobal C10 & 15–17, Loyalty Islands and Vanikoro G35 & 38 (olive); Bougainville and Malaita C9 & 12, northern Australia E22–23, Tasmania and southern Australia F28–30, New Caledonia, and New Hebrides from Erromango northwards G34, 37a–c & e (considerably greyer than standard).

(10) GORGET YELLOW-WASHED. Choiseul to Russel Islands, central Solomons, Rennell and San Cristobal C10 & 13–17; Loyalty Islands and Vanikoro G35 & 38; Babar and Tenimber Isles H40 & 42; Louisiades H47.

(11) BREAST AND FLANKS OLIVE. Morotai to Batjan B6–7; Choiseul and Kulambangra to Florida, and Rennell C10 & 15–16 (pale); Snow Mountains E27 (pale, confined to narrow band behind gorget); *P. soror* (pale); *P. schlegelii* (deep in Snow Mountains and south-eastern New Guinea).

Many forms have a combination of carotenoid and phaeomelanins on the underparts, but this ventral olive is rare.

(12) UNDERPARTS UNIFORM. Koro and Vatu vara D20b–21, and individuals on Ovalau and Taviuni D18b & 20a; Tenimber Isles H42; Mussau and Lihir H48d–49; southern Fiji H54–56.

On Ceram and Buru H43–44 and in the Bismarcks H48a–c, the gorget is little darker than the throat and mid-belly.

(13) BELLY WASHED WITH MELANINS. Islands in Flores Sea A4 (pinkish); Bougainville, Guadalcanal and Malaita C9 & 11–12 (greyish or rufous buff); Rendova and Tetipari C14 (deep rufous); Fiji D18–21, H54–56 (greyish on Viti Levu and Vanua Levu D18a & 19a, cinnamon on Koro, Vatu vara and in southern Fiji D20b–21 & H54–56, individually variable between Koro and the large islands D18b & 19b–20a); south-western and South Australia F28a–b (pinkish), Tasmania, Victorian mallee and northern Queensland F28c, 29 & 31b (buffy); New Caledonia G34 (pale buffy); Timor H39 (pinkish); Damar, Tenimber Isles, Ceram to Sula Isles, Bismarcks except Tabar H41–45 & 48–49 (brownish, more or less mixed with yellow).

(14) BREAST AND BELLY DEEP YELLOW. Morotai to Obi B6–8 (deepest on Obi B8); Choiseul and Vella Lavella to Florida, and San Cristobal C10, 13, 15 & 17; northern Australia, *dahli* and Snow Mountains E23, 25 & 27; Loyalty Islands and Vanikoro G35 & 38; Babar H40, Peleng Isles H46, Louisiades H47, Tabar H50, Manus H51, Utupua H53, Tonga H57; *P. soror*; *P. schlegelii*.

(15) BREAST AND BELLY SCARCELY YELLOW. Sumbawa to Alor and islands in Flores Sea A3–4; Bougainville, Guadalcanal and Malaita C9, 11 & 12 (juveniles may be yellower); Fiji except Kandavu D18–21, H55–56; midwestern Australia E22a–c; Tasmania and southern Australia F28–30; Malekula and Santo G37d; Timor, Damar and Buru H39, 41 & 44.

(16) UNDER TAIL-COVERTS NOT YELLOW. Tasmania and southern Australia F28–30.

Here the female plumage is almost devoid of carotenoid, except for a circlet of pale yellow feathers at the vent.

(17) CAP OLIVE. Solomons C9–17 (may be obscured by heavy rufous wash).

(18) CAP GREY. Salayer A5; Morotai to Batjan B6–7; midwestern Australia to small islands in the Bismarcks E22–25; Tasmania, southern and eastern Australia, Lord Howe and Norfolk Island F28–33; Vanikoro G38; Tabar H50, Lau archipelago and Tonga H56–57; *P. schlegelii* east of the Vogelkop 2–3.

(19) AURICULARS GREY. Morotai to Batjan B6–7; Vanikoro G38; *P. schlegelii* east of the Vogelkop 2–3.

(20) MANTLE GREY. Tasmania and Victoria F29–30a (wholly grey); south-western and South Australia and New South Wales F28 & 30b (individuals with olive wash on rump or scapulars); midwestern Australia E22a–c (rump olive); north-western Australia E22d (rump and lower back olive).

(21) TAIL GREY. Tasmania and southern Australia F28–30.

(22) MANTLE PURE OLIVE OR GREY (WITHOUT PHAEOMELANINS). Sumba and Salayer A1 & 5; Morotai to Batjan B6–7; San Cristobal C17; midwestern Australia to *dahli* and Snow Mountains E22–25 & 27; Vanikoro G38; Tabar H50; Tonga H57; *P. schlegelii* in Cyclops Mountains 2.

(23) UPPERPARTS BROWN. Northern and central Fiji D18–21 ; Ceram H43, Louisiades H47, Mussau H48d, Lihir H49.

The mantle is distinctly brownish-olive on Aneitum and from Mai to Santo G36 & 37c–d, from Timor to the Tenimber Isles H39–42 (tail pure olive on Babar H40), from Buru to the Peleng Isles H44–46, in the rest of the Bismarcks and on Manus H48a–c & 51, on Ndeni, Santa Cruz islets and Utupua H52–53, in southern Fiji H54–56, and in *P. soror* in the Vogelkop 1.

(24) UPPERPARTS SOMETIMES RUFOUS-WASHED. Choiseul to Guadalcanal, and Vella Lavella to Tetipari C10–11 & 13–14 ; northern and central Fiji D18–21.

(25) WINGS RUSSET-EDGED. Solomons except San Cristobal C9–16 (mixed with olive from Choiseul and Kulambangra to Florida C10 & 15) ; northern and central Fiji D18–21 (mixed with olive on Koro D20b).

(26) TAIL PARTLY BLACK. San Cristobal C17 ; north-western and northern Australia, *dahli* and Snow Mountains E22d–23, 25 & 27 ; *P. soror.*

The variable hybrid populations on the small islands off Shortland E26 have largely been omitted from the character-geography. They are discussed on p. 156.

NATURAL GROUPS

Co-variation and character-complexes

Single characters might be used to link populations into as many sets of overlapping assemblages as there are characters under consideration. If these bore no relation to one another, or were strictly correlated with environmental features, little could be inferred about relationships and evolutionary history. In many groups, the few characters available in ordinary museum material may be too sporadic or too liable to parallel evolution to be helpful. But where there are many characters, capable of independent variation and not exclusively related to environmental differences, major discontinuities can be detected despite the local elimination or independent origin of single characters.

In the *P. pectoralis* superspecies, both the male and the female patterns are subject to a great deal of variation. The distribution of each character is different, so that all are at least partly independent. They are of very unequal systematic value ; great when their boundaries coincide with major discontinuities in the constellation of characters, small when they occur in forms not otherwise connected. Thus the loss of the male gorget is an important character, since in other respects also the Malaitan race C12 connects with those of northern Fiji D18–19, and these with *P. flavifrons*. Hen-feathering, on the other hand, is unimportant, since the hen-feathered races A5, C16 and F33 resemble, not one another, but the females of neighbouring dimorphic forms. A character may be important in one part of the range though not in another. For example, grey-winged males distinguish the closely-related forms (group E) which range from midwestern Australia to the Bismarcks E22–25, from others whose ranges they approach closely and whose males are otherwise very similar (F31, H47–50, *P. soror* 3) : but such grey wings are found also in eastern Fiji D19 & 21 & H56, in Tasmania and southern Australia F28–30, on Damar H41 and in *P. soror* 2 ; and not in the Snow Mountain race E27, which also belongs to group E.

Striking variants of the male pattern, which seem to be relatively stable, mostly mark off local groups of populations with rather compact geographical boundaries. However, many of them are associated with very different character-complexes in different parts of the species range, and even locally a single character is seldom precisely co-extensive with the complex. The major discontinuities cannot be adequately defined by using these few more or less clear-cut characters alone. The much greater number of obviously quantitative differences must be considered as well. Although all are liable to parallel evolution and extensive intergradation, discontinuities are marked by concordant changes in a number of characters.

Intergradation

Few of the discontinuities are sharply defined. Almost everywhere, very distinct forms are connected by populations which are intermediate in range and character. Sometimes the changes are more or less regular in all the characters concerned, sometimes they are abrupt or out of step. At a few points (p. 160) the intermediate populations are highly variable, and it is clear that the intergradation is secondary—forms which differentiated in isolation have met and exchanged genes in a hybrid zone. Where the individual populations do not show exceptional variability, the intergradation may be primary or secondary. Primary intergradation could result from selection in relation to environmental gradients, or from incomplete isolation between diverging populations, or (conceivably) from the expression of orthogenetic trends after successive expansions of range (cf. Mayr & Moynihan, 1946, 1). Secondary intergradation without increased variability would imply that the hybrid populations had been stabilized by subsequent selection. In *P. pectoralis* the geographical patterns of intergradation, and the characters involved, make it seem highly probable that the most striking examples of intergradation have resulted from the hybridizing of differentiated forms, with subsequent stabilization (p. 160). In other areas, however, character gradients seem to be correlated with climatic differences (p. 186).

Subspecies–groups

There are all degrees of phenotypic discontinuity, from differences between individuals of the same population upwards. The precise scope and rank of any natural group of populations must be to some extent a matter of opinion, except that sympatry introduces an objective criterion at the species level. The useful scope of the subspecies is discussed on p. 175. For convenience, such a richly diverse species as *P. pectoralis* must be broken up into subspecies-groups. These will not be of equal distinctiveness and homogeneity. Where a rather compact range is occupied by closely related forms, yet divided by considerable discontinuities, the number of groups to be recognized is to some extent a matter of choice. For example, the Australian subspecies-groups E and F might be combined into one, since the differences between them are much less sharp than those which mark off some other groups (cf. Mayr, 1954*a*, 19).

Where unlike forms intergrade they should not be separated if the connecting cline seems to be environmentally determined. Mathews (1930) not only removed the

Northern Australian group E from *P. pectoralis* but split it into two species, on the basis of characters which strongly suggest selective adaptation to climate (p. 187). But where the intergradation seems to be secondary and the end-forms are sufficiently unlike, they should be separated even though the position of the dividing line will have to be arbitrarily decided.

The situation in *P. pectoralis* is extremely complex. It seems to result from great plasticity in plumage characters combined with unusual ethological and genetic tolerance, and high mobility in successive waves of colonization combined with philopatry in local populations. As a result, very unlike forms have evolved and then met and interbred freely, and the resulting character-gradients mimic the true adaptive clines which also occur. It is unlikely that two students will ever agree on every detail of this confused situation.

In the following descriptions, the superspecies has been divided into eleven groups. These are treated in an order determined by higher grouping according to characters and trends (p. 168), regardless of the implications of sympatry and intergradation. The use of binomens for some of these groups (e.g. " *P. schlegelii* ") and informal designations for others (e.g. " Solomons group C ") anticipates the findings of later sections. A description of the divergence of each group as a whole from the standard patterns is followed by character-geographies of departures from the group patterns so determined. In general, group patterns have been arrived at (like the standard patterns of the whole superspecies) by combining those characters which are found in a majority of the contained forms, excluding those which are obviously intermediate with other groups. But in the Lesser Sunda Isles, Moluccas and Fiji, it seems clear that few forms have escaped contamination by gene-exchange. Here the group patterns are taken to be those of the apparently pure forms A1, B6–7, and D18a & 19a.

P. schlegelii (Text-fig. 3, p. 167)

Small birds. Male chin black, throat-patch small; gorget very broad, fore-edge defined by white feathers; breast, flanks and belly rufous-washed; mantle very dark; wing, upper tail-coverts and tail black. Female throat barred grey and white, gorget grey, breast and flanks olive; belly lemon-yellow; cap and auriculars grey, mantle pure olive.

MALE VARIATION. Throat-patch larger and gorget narrower in Vogelkop 1. Rufous very deep in south-eastern New Guinea 3b, paling steadily westwards to 3a; much paler in Vogelkop and Cyclops Mountains 1–2.

FEMALE VARIATION. Throat white with grey bars, gorget and breast pale in Vogelkop and Cyclops Mountains 1–2; throat grey with white bars, gorget and breast dark from Weyland Mountains to south-eastern New Guinea 3.

Greys and olives brownish in Vogelkop 1.

Lesser Sundan group A (Text-fig. 2, p. 161)

Very small birds. Male chin black, throat-patch small and separated by black feathers from auriculars; gorget narrow, fore-edge defined by white feathers; breast, belly and flanks rufous-washed; collar narrow and olive-washed; upper tail-coverts and tail black. Female throat whitish ; gorget greyish, pale and vague ; cap sandy-grey ; mantle pale sandy-olive.

MALE VARIATION. Hen-feathered on Salayer A5—male differs from female in larger throat-patch, greyer gorget and cap, grey auriculars, and darker and greener mantle.

Throat-patch touches auriculars from Java to Alor and in Flores Sea A2–4 ; patch not small, and fore-edge of gorget with black tips, in Flores Sea A4.

Rufous pale on belly in Java A2a, more so on Bali A2b, restricted to band behind gorget from Sumbawa to Alor A3, very pale and barely detectable below breast in Flores Sea A4.

Wing black and mantle mottled with black in Flores Sea A4 (individually variable).

Tail with narrow pale tips from Java to Alor and in Flores Sea A2–4.

FEMALE VARIATION. Throat pure white in Flores Sea and on Salayer A4–5, pinkish-buff from Java to Alor A2–3.

Gorget rather pinkish from Java to Alor and on Salayer A2–3 & 5 ; breast and belly uniformly pinkish in Flores Sea A4.

Breast and belly with very little yellow from Java to Alor and in Flores Sea A2–4.

Cap almost pure grey and mantle pure olive on Salayer A5, distinctly sandy from Sumbawa to Alor and in Flores Sea A3–4, less so on Sumba and Java A1–2.

Except for their smaller size, females from the Flores Sea A4 are very like those of Timor H39.

Moluccan group B (Text-fig. 2)

Medium-sized to large birds. Male chin black ; throat feathers long, partly covering gorget and cutting it off from auriculars ; gorget narrow from side to side, without black tips in the fore-edge ; upper tail-coverts and tail black. Female throat barred grey and white, gorget grey, breast and flanks pale olive ; belly lemon-yellow ; cap and auriculars grey, mantle pure olive.

SIZE VARIATION. Large birds on Ternate, Tidore and Obi B7–8.

MALE VARIATION. Chin white, throat feathers shorter, and tail with narrow and obscure pale tips on Obi B8.

FEMALE VARIATION. Throat-bars and gorget buff, breast and flanks ochraceous, belly golden-yellow, cap and mantle brownish on Obi B8.

Greys slightly paler and olives yellower on Ternate and Tidore B7 than from Morotai to Batjan B6.

The Obi form B8 is precisely intermediate between those of Ternate and Tidore B7 and Ceram H43, except that the female belly is deeper yellow than in either.

Solomons group C (Text-fig. 2)

Very large birds. Male chin black ; throat-patch yellow, rather small ; gorget broad, fore-edge defined by yellow feathers ; collar washed with olive. Female bill pale ; gorget broad and vague ; breast and flanks washed with melanins ; cap olive ; wing-feathers edged with russet.

SIZE VARIATION. Small birds on Rennell and San Cristobal C16–17, large (not very large) from Vella Lavella to Gatukai C13 & 15.

MALE VARIATION. Hen-feathered on Rennell C16—male almost indistinguishable from female, but with slightly more carotenoid on the average.

Chin yellow on San Cristobal C17.

Throat-feathers long (extending behind auriculars), gorget very broad on Vella Lavella and Ganonga C13.

Gorget absent, but throat-feathers sometimes black-fringed, on Malaita C12.

Some black tips in fore-edge of gorget on San Cristobal C17.

Rufous patch below gorget on Santa Anna C17b and in individuals on San Cristobal C17a.

Head olive with blackish lores and auriculars on Santa Anna C17b, varies from olive (auriculars brownish) to black on San Cristobal C17a.

Collar absent on Vella Lavella and Ganonga C13 ; reduced to a trace on Malaita and from Kulambangra to Gatukai and Tetipari C12 & 14–15 ; reduced to a trace on the hind-neck, but with broad patches laterally, on San Cristobal C17.

Entire upperparts and flanks black on Vella Lavella and Ganonga C13 (individuals on Ganonga C13b have narrow olive edges on the wings) ; wing black and mantle more or less mottled with black on Rendova and Tetipari C14 ; centres of mantle-feathers blackish, and olive dark greenish, from Kulambangra to Gatukai C15 ; olive rather greenish on San Cristobal C17.

Upper tail-coverts olive from Kulambangra to Gatukai and on San Cristobal C15 & 17 ; olive edges broad on Malaita C12. Tail more or less olive on San Cristobal C17.

FEMALE VARIATION. Bill straw-coloured from Kulambangra to Guadalcanal and Rennell C10c–11 & 15–16 ; blackish brown elsewhere.

Individuals on Vella Lavella C13a are melanistic, with black gorgets and more or less black upperparts.

Underparts faintly washed with yellow, cheeks yellower than throat, on Bougainville and Guadalcanal (juveniles sometimes much yellower) and Malaita C9, 11 & 12 ; yellow pale on Rendova, Tetipari and Rennell C14 & 16 ; lemon-yellow elsewhere (when unmixed with melanins).

Throat faintly barred on Malaita C12 ; underparts (except mid-belly) conspicuously shaft-streaked on Malaita C12, more faintly on Bougainville, Choiseul and Guadalcanal, and from Kulambangra to Gatukai C9–10a, 11 & 15.

Gorget greyish on Bougainville and Malaita C9 & 12 ; olive from Choiseul and Kulambangra to Florida, and on Rennell and San Cristobal C10 & 15–17 (fairly narrow and distinct on San Cristobal C17) ; rufous on Guadalcanal and from Vella Lavella to Tetipari C11 & 13–14.

Underparts washed with deep rufous on Rendova and Tetipari C14 ; rufous very variable in extent and depth on Vella Lavella and Ganonga C13 ; confined to gorget, breast and flanks on Ysabel and Guadalcanal C10b & 11 (deep, pale or absent), and Choiseul, Russel Isles and Rennell C10a & c & 16 (pale).

Breast and flanks pale olive from Kulambangra to Gatukai and on Rennell C15–16, and in individuals from Choiseul to Florida C10.

Cap citrine, mantle olive on San Cristobal C17 ; cap brownish or rufous olive, mantle olive from Kulambangra to Gatukai and on Rennell C15–16 ; cap brownish citrine, mantle citrine from Buka to Malaita C9–10 & 12 (sometimes with a rufous wash on Ysabel C10b, less common on Choiseul C10a); cap rufous, scapulars and mantle strongly washed with rufous (most consistently on Rendova and Tetipari C14) on Guadalcanal and from Vella Lavella to Tetipari C11 & 13–14. Indications of a collar from Buka to Guadalcanal and on Vella Lavella and Ganonga C9–11 & 13.

Olive dark from Kulambangra to Gatukai C15, darker still on Rennell C16.

Olive dull (little carotenoid) on Rennell C16; richer on Guadalcanal, Rendova and Tetipari C11 & 14; richer on Bougainville and from Kulambangra to Gatukai C9 & 15; richer from Choiseul to Malaita and on Vella Lavella and Ganonga C10, 12 & 13; rich on San Cristobal C17.

Wing-feathers edged with olive on San Cristobal C17; russet mixed with olive from Russel Isles to Kulambangra C10c & 15, less strongly from Choiseul to Florida C10a–b.

Tail pure olive, with variable black subterminal patch, on San Cristobal C17; citrine from Buka to the central Solomons and Guadalcanal C9, 13–15 & 10c–11; olivaceous brown from Choiseul to Malaita C10a–b & 12; dull brown on Rennell C16.

Fijian group D (Text-fig. 2)

Medium-sized birds. Male chin and throat yellow; no gorget; forehead yellow; black of cap continued on to hind-neck, collar reduced to a trace; olive very dark; upper wing-coverts yellow-edged; upper tail-coverts olive; olive tips of tail-feathers dull but wide. Female forehead, circumoculars, cheeks and under tail-coverts faintly washed with yellow, underparts otherwise without carotenoid (buffy-grey, with throat and mid-belly slightly paler); underparts streaked with brown, and throat and breast barred also; upperparts dull olive-brown, wing-feathers edged with dark russet; individuals are dark rufous all over.

MALE VARIATION. Underparts lemon-yellow on Viti Levu and Ovalau D18, orange-yellow elsewhere.

More or less complete gorget, individually variable, on Ovalau and from south-western Vanua Levu to Kio D18b & 19b–c; gorget complete (though somewhat irregular) on Taviuni, Koro and Vatu vara D20–21.

Breast, belly and under tail-coverts washed with brown on Vatu vara D21; under tail-coverts ochraceous on Koro D20b, decreasingly so towards Vanua Levu D20a to 19b.

Collar narrow but uninterrupted on Vatu vara D21.

Wing-quills edged with greyish on Vanua Levu and Vatu vara D19 & 21, becoming more olive eastwards, towards Viti Levu and Koro D18 & 20.

Upper tail-coverts with black centres on Koro and (larger) on Vatu vara D20b–21.

FEMALE VARIATION. Bill brown on Rambi and Kio D19c.

Underparts evenly-coloured on Koro and Vatu vara D20b & 21; mottling becomes more common and emphatic towards the large islands D18b to a, and 20a to 19a. Ground-colour of underparts cinnamon on Koro D20b and (rather paler) Vatu vara D21, individually variable, becoming greyer, towards the large islands D18b to a, and 20a to 19a.

Forehead, circumoculars and cheeks not yellow on Koro and Vatu vara D20b–21; increasingly so towards the large islands D18b to a, and 20a to 19a.

Females on Koro and Vatu vara D20b–21 are very like those in southern Fiji H54–56.

P. flavifrons (Text-fig. 5, p. 173)

Small birds. Male chin dull black, throat dull black with broad yellow or white tips; no gorget ; underparts lemon yellow ; forehead yellow or white ; upperparts dull black (slightly washed with olive), primaries with obscure narrow greyish edges. Female cock-feathered—like the male, but throat pale grey with narrow yellow or white tips, forehead blackish (with or without a yellow wash).

INDIVIDUAL VARIATION. The tips of the throat feathers are usually yellow, but may be white ; two specimens in the British Museum (Natural History) have mixed yellow and white tips. Some white-throated birds have the forehead white (in females, without a yellow wash). The distribution of these phases in the collections of the British Museum (Natural History), and the American Museum of Natural History (from Mayr, 1932*b*), is shown in Table II : there is no evidence of a significant difference in representation of the colour phases, either between the sexes or between Savaii and Upolu. All the B.M. (N.H.) specimens are from Upolu.

TABLE II.—*Colour Phases in* P. flavifrons.

	Forehead.	
Throat.	Yellow.	White.
Yellow	48	—
Yellow and white . .	2	—
White	8	9

P. soror (Text-fig. 3)

Small birds. Male throat-patch rather small ; gorget narrow ; underparts lemon-yellow ; breast and flanks faintly olivaceous ; collar reduced to a trace ; mantle very dark greenish olive ; edges of wing quills greyish ; upper tail-coverts olive, tail partly olive. Female throat-patch white and small ; gorget narrow, clear and brownish ; breast and flanks pale citrine, yellow wash extending high on breast ; belly pale lemon-yellow ; cap olivaceous-brown ; tail partly black.

MALE VARIATION. Mantle increasingly golden-olive towards the west 3 to 1. Wing quills greyest in the centre 2.

Tail olive, with a variable black subterminal patch, in the west and east 1 & 3 ; black, with wide olive edges basally, in the centre 2.

FEMALE VARIATION. Upperparts much browner in Vogelkop 1 ; increasingly purer olive towards the east 2 to 3.

Northern Australian group E

Very small to medium-sized birds. Male throat-feathers white to their bases ; edges of wing-quills grey ; edges of upper wing-coverts yellow ; primary-coverts black. Female throat white, with barring ; gorget well defined, buffy-grey ; breast, flanks and belly whitish to golden-yellow, without melanins; cap rather pure grey, mantle pure olive (or grey); tail partly black.

SIZE VARIATION. Very small birds in mid-western Australia E22a–c, size increasing through north-western Australia E22d to small in northern Australia and southern New Guinea E23–24. Like the Snow Mountain birds E27, those grouped together as *dahli* E25 are mostly medium-sized—but there is considerable variation between the scattered populations, with the birds of Fergusson E25c (and Teste and Long Islands E25b & d) rather large, and those of south-eastern New Guinea and Witu E25a & e apparently rather small.

MALE VARIATION. Throat-feathers grey-based in Snow Mountains E27 (Text-fig. 3).

Breast and belly lemon-yellow in mid-western Australia E22a, gradually becoming deeper northwards E22b to d, golden-yellow from northern Australia eastwards E23–27.

Collar narrow in midwestern Australia E22a (widening northwards E22b to 23), and Snow Mountains E27.

Mantle greenish-olive in midwestern Australia E22a (becoming yellower northwards E22b to 23), and Snow Mountains E27.

Edges of wing-quills olive in Snow Mountains E27.

Primary-coverts olive in mid-western and north-western Australia and Snow Mountains E22 & 27; sometimes with very narrow pale edges from northern Australia to southern New Guinea E23 to 24.

Upper tail-coverts olive in mid-western and north-western Australia E22.

Tail with broad olive edges basally in midwestern Australia E22a, decreasing northwards E22b to d.

FEMALE VARIATION. Females from Teste and Fergusson E25b–c are unknown.

Throat unbarred in mid-western Australia E22a–c, barring pale in north-western and northern Australia E22d–23; throat and gorget shaft-streaked (in addition to barring) from Cape York to southern New Guinea E24 (faintly) and in *dahli* and Snow Mountains E25 & 27.

Breast and flanks pale olivaceous in Snow Mountains E27; ochraceous from Cape York to southern New Guinea E24.

Breast and belly whitish and under tail-coverts pale yellow in mid-western Australia E22a–c; breast and belly pale yellow, under tail-coverts lemon-yellow, in north-western Australia, and from Cape York to southern New Guinea E22d & 24; underparts lemon-yellow in northern Australia E23, golden-yellow in *dahli* and Snow Mountains E25 & 27.

Cap brown in Snow Mountains E27.

Mantle grey, only rump olivaceous, in mid-western Australia E22a–c, becoming olive northwards E22d to 23. Olive bright in Snow Mountains E27.

Edges of wing feathers, rump and base of tail brownish on Witu, Malie and Nissan E25e & j–k.

Tail olive in mid-western Australia, and from Cape York to southern New Guinea E22a–c & 24; with a variable amount of black in north-western and northern Australia E22d–23; more than half black in *dahli* E25; black with olive edges in Snow Mountains E27.

Mayr has shown (1932*a*) that the birds on small islands west of Shortland E26 form a hybrid population. The nine known males show almost every degree of intermediacy between *dahli* E25 and the Bougainville-Shortland race C9—except that they do not have black chins like those of the Solomons group C. In this series the largest birds have the yellowest throats, and the smallest ones the whitest. Other characters seem to vary independently, so far as can be judged from this short series. There is rather less variation between the nine females, which are also intermediate between those of E25 and C9.

The females from Cape York to southern New Guinea E24 differ from those on either side (E23 & 25) in characters which approach those of the Queensland form F31—breast and flanks ochraceous, little ventral yellow, tail without black (Mayr, 1954a).

The Louisiades form H47 is intermediate between groups E and H. It is here placed in the latter because the male has olive edges to the wings, and the female is brownish ; but the white throat, sharp and narrow gorget and bright yellow underparts of the female are untypical of group H. The Tabar form H50 may be similarly intermediate (p. 164).

Southern Australian group F

Large birds, with long wings and tails, small bills and soft plumage. Male breast and belly lemon-yellow ; collar rather narrow and washed with olive ; upper wing-coverts yellow-edged ; upper tail-coverts olive, base of tail olive or grey. Female throat barred ; gorget, breast and flanks buffy-grey, belly more or less washed with melanins ; yellow absent from underparts, or only in under tail-coverts ; cap grey, mantle dull sandy-olive.

SIZE VARIATION. Large birds with long tails and very small bills in Tasmania F29, size and relative tail-length decreasing and bills lengthening northwards—smallest birds near Cairns F31b, longest bills on Lord Howe and Norfolk Islands F32–33.

MALE VARIATION. Hen-feathered on Norfolk Island F33—indistinguishable from female.

Yellow somewhat paler from south-western Australia to Tasmania F28–29.

Collar broader and clearer on Lord Howe F32.

Wing quills blackish brown with grey edges in Tasmania F29, centres blackening and edges becoming more olive northwards F28 and 30 to 31.

Tail without black in Tasmania F29 ; about one-third black from south-western Australia to South Australia F28a–b ; increasing through Victorian mallee F28c to two-thirds black in south-eastern Australia F30 ; two-thirds black on Lord Howe F32 (olive tips very wide) ; mainly black, olive varying from wide edges to a wash at the extreme base, in Queensland F31 (averaging blacker near Cairns F31b).

Pale part of tail grey in Tasmania and southern Australia F28–30a ; olive elsewhere, but often greyish near Cairns F31b.

FEMALE VARIATION. Belly pinkish from south-western Australia to South Australia F28a–b, fading to buffy in Victorian mallee, Tasmania and near Cairns F28c–29 & 31b ; whitish in south-eastern Australia F30 ; often faintly yellowish in southern Queensland F31a, and always on Lord Howe F32; distinctly yellow on Norfolk Island F33.

Under tail-coverts whitish in Tasmania and southern Australia F28–30.

Upperparts rather brownish in Tasmania F29, and more or less brownish in most individuals near Cairns F31b; rather pure grey in south-western Australia F28a.

Mantle grey in Tasmania F29; sometimes with a faint olive wash in southern Australia F28 & 30; dull olive elsewhere.

Tail grey in Tasmania and southern Australia F28–30; dull olive near Cairns F31b; olive elsewhere.

Southern Melanesian group G

Small birds. Male gorget narrow; breast and belly lemon-yellow; collar narrow and washed with olive; centres of wing-feathers blackish-brown; upper tail-coverts and tail olive. Female throat white; gorget greyish; breast and belly without melanins.

Size variation. Very large birds on Loyalty Islands G35.

Male variation. Lateral throat feathers long, separating gorget from auriculars, on New Caledonia G34 (Text-fig. 5).

Gorget dull black, and very narrow, on New Caledonia G34; dull black on Aneitum G36; rather broad on Vanikoro G38.

Pale rufous patch below gorget on New Caledonia G34.

Flanks and under tail-coverts ochraceous, rump, tail and edges of secondaries washed with brownish, in individuals on Aneitum G36.

Breast and belly golden-yellow on Loyalty Islands G35.

Cap and auriculars grey on New Caledonia G34; dull black, cap more or less scalloped with olive, on Aneitum G36.

Collar reduced to a trace on New Caledonia G34, very narrow on Erromango G37a.

Mantle greenish-olive on Erromango, and from Raga to Vanikoro G37a & 37e–38; golden-olive on Loyalty Islands, and Malekula and Santo G35 & 37d.

Upper tail-coverts black-centred, tail black, on Vanikoro G38; tail with black patches (on inner webs of all but central quills) from Erromango to Banks Islands G37.

Female variation. Throat and gorget shaft-streaked on Vanikoro G38.

Gorget olive on Loyalty Islands and Vanikoro G35 & 38; greyest on Erromango, Efate and Banks Islands G37a–b & f; brownish on Aneitum G36.

Gorget extends into buffy-grey wash on breast and belly on New Caledonia G34.

Underparts golden-yellow on Loyalty Islands G35, lemon-yellow on Vanikoro G38; elsewhere, under tail-coverts pale yellow, breast and belly faintly washed with yellow (palest on Malekula and Santo G37d).

Cap and auriculars grey on Vanikoro G38; cap greyish on Efate and Banks Islands G37b & f; brownish on Aneitum G36.

Mantle pure golden-olive on Loyalty Islands G35, pure greenish-olive on Vanikoro G38; elsewhere dull olive, purest on Efate and Banks Islands G37b & f, brownish on Malekula and Santo G37d; very brown on Aneitum G36.

Tail and edges of secondaries browner than mantle on Loyalty Islands G35, somewhat so on Aneitum and Erromango G36–37a.

JUVENILE VARIATION. Throat lemon-yellow on Vanikoro G38, sometimes yellow-washed in New Hebrides (recorded from G37c & f by Mayr, 1932*b*). Juveniles on Vanikoro G38 are remarkably like those on San Cristobal C17, except for the shaft-streaking of their throats and gorgets.

The New Hebrides G36–37 are a region of incipient subspeciation, with the females of almost every island distinguishable in series (Mayr, 1932*b*). The Aneitum population G36 is rather distinct, and that on Erromango G37a more so than the others.

Widespread group H (close to standard patterns, Text-fig. 1)

Small to very large birds. Male of standard pattern. Female underparts rather uniform, brownish, with little yellow; upperparts brownish, cap not contrasting, edges of wing feathers distinctly browner than mantle.

SIZE VARIATION. Very large birds on Tenimber Isles, Lihir and Tonga H42, 49 & 57; large on Tabar and Lau archipelago H50 & 56; small on Timor and Damar, Sula and Peleng Isles, large islands in the Bismarcks, and Kandavu H39, 41, 45–46, 48 & 54.

MALE VARIATION. Chin and throat black in Tonga H57 (Text-fig. 5); yellow on Tenimber Isles H42.

Throat-feathers long, cutting gorget off from auriculars (fore-edge of gorget defined by white feathers) on Ceram, and Ndeni and Santa Cruz islets H43 & 52; gorget very narrow near auriculars, with few black tips, on Buru H44.

Gorget streaked with white on Babar H40; dull black and very narrow on Kandavu H54, narrow on Ngau H55.

Underparts lemon-yellow from Timor to Tenimber Isles and on Utupua, Kandavu and Tonga H39–42, 53–54 & 57; orange-yellow in Louisiades and on Lihir and Manus H47, 49 & 51.

Under tail-coverts ochraceous on Ngau H55.

Upperparts (except for narrow olive edges on wing-feathers) black on Ndeni and Santa Cruz islets H52; mantle mottled with black in Lau archipelago H56, somewhat so on Ngau H55.

Primary-coverts black on Ceram and Buru, Ndeni and Santa Cruz islets, and Lau archipelago H43–44, 52 & 56.

Collar absent on Ndeni and Santa Cruz islets H52; reduced to a trace on Tenimber Isles H42, and Ngau and Lau archipelago H55-56 (black of cap extends on to hindneck); washed with olive from Timor to Damar, in the Louisiades and on Utupua and Kandavu H39–41, 47 & 53–54.

Olive dark and greenish on Buru, Ngau and Lau archipelago H44 & 55–56; dull on Kandavu H54.

Olive washed with brownish (especially on rump, tail and edges of secondaries) on Ceram and Louisiades H43 & 47.

Edges of wing quills grey on Damar H41, and greyish in Lau archipelago H56.

Upper tail-coverts olive on Timor, Tenimber Isles, Louisiades, Kandavu and Tonga

H39, 42, 47, 54 & 57; black from Ceram to Peleng Isles H43–46 (very narrow olive edges on Buru H44).

Tail olive on Timor and western Louisiades H39 & 47a; olive with blackish subterminal patches on Misima and Kandavu H47b & 54; olive basally on Babar and Rossel H40 & 47c; with broad olive edges basally on Damar H41.

Pale tip of tail very broad and yellowish in Tonga H57.

FEMALE VARIATION. Throat white on Timor and Babar, Louisiades and Utupua H39–40, 47 & 53; whitish on Damar, Ceram, Sula and Peleng Isles, Tabar, Manus, Ndeni and Santa Cruz islets H41, 43, 45–46 & 50–52.

Throat washed with yellow on Tenimber Isles H42.

Throat barred on Damar, Sula and Peleng Isles H41 & 45–46, and faintly in Tonga H57.

Throat and gorget streaked on Manus H51, and faintly on Tabar H50.

Underparts uniformly cinnamon in southern Fiji H54–56 (very richly so on Ngau H55). Gorget scarcely darker than throat and belly on Mussau and Lihir H48d–49; little darker on Tenimber Isles, large islands of the Bismarcks, and Ndeni and Santa Cruz islets H42, 48a–c & 52. Gorget little darker than breast, but greyer, on Timor and Damar and from Ceram to Peleng Isles H39, 41 & 43–46. Gorget pale and narrow on Babar and Louisiades H40 & 47 (vinous), Tabar, Manus and Tonga H50–51 & 57 (cinnamon); broad on Utupua H53 (dark brown).

Breast and belly without melanins in Louisiades H47; belly without melanins, breast faintly cinnamon on Tabar and Tonga H50 & 57; belly without melanins, breast and flanks brownish on Utupua H53; breast and belly faintly washed with cinnamon on Babar and Manus H40 & 51.

Breast and belly without yellow on Ngau and Lau archipelago H55–56; faintly washed with yellow on Timor, Damar, Buru and Kandavu H39, 41, 44 & 54, more strongly on Tenimber Isles, Ceram and Sula Isles H42–43 & 45; yellow pale on Babar, Bismarcks except Tabar, and Ndeni and Santa Cruz islets H40, 48–49 & 52; deep in Peleng Isles and Louisiades H46 & 47, and especially on Tabar and Manus H50–51.

Cap grey on Tabar, Ngau and Tonga H50, 55 & 57; distinctly greyer than mantle on Manus, Utupua, Kandavu and Lau archipelago H51, 53, 54 & 56; distinctly browner than mantle on Bismarcks except Tabar H48–49.

Mantle bright citrine on Tabar, Manus and Tonga H50–51 & 57; dull sandy-olive on Timor, Damar, Tenimber Isles, Kandavu and Lau archipelago H39, 41–42, 54 & 56; brownish olive on Babar H40 (tail pure olive), Peleng Isles, Louisiades, large islands of the Bismarcks, Utupua and Ngau H46, 47, 48a–c, 53 & 55; browner and duller from Ceram to Sula Isles and on Ndeni and Santa Cruz islets H43–45 & 52; olive-brown on Mussau and Lihir H48d–49.

Edges of wing feathers scarcely browner than mantle on Tabar, Manus and Tonga H50–51 & 57.

Not only are the distinctive characters of the group few and slight, but most of the forms are intermediate in some respects with neighbouring groups. Besides penetration by characters proper to other groups, intermediate forms seem to be liable to special changes (p. 165). The wide range of this group has enabled it to meet and intergrade with five of the seven other subspecies-groups, and there seems to have been gene-flow into it in the following areas:

From group A to Timor and Babar H39–40.
From group B to Ceram, Peleng and Sula Isles H43 & 46–45.
From group D to southern Fiji H54–56.
From group E to Louisiades H47 (and possibly Damar, Tabar and Manus H41 & 50–51).
From group G to Utupua H53.

When the effects of this gene-exchange have been allowed for, three forms stand out conspicuously from the remarkably uniform remainder:

Tenimber Isles H42 (very large, throat yellow).
Ndeni and Santa Cruz islets H52 (male upperparts black, throat-feathers long).
Tonga H57 (very large, male throat black, female with little brown and much yellow).

INTERGRADATION AND BRIDGELESS GAPS

Gene-exchange between subspecies-groups

The eight subspecies-groups of *P. pectoralis* approach one another in several areas, in all of which there are signs of intergradation between them (Text-fig. 8). Groups A and H intergrade in the Lesser Sunda Isles, B and H in the southern Moluccas, C and E in the western Solomons, C and G in the eastern Solomons, D and H in central Fiji, E and F in southern New Guinea, E and H in the Louisiades, and G and H in the Santa Cruz archipelago. In most of these areas, it is not immediately obvious whether the intergradation is primary or secondary.

Only in the western Solomons is there indisputable evidence of hybridization between very dissimilar forms. The populations on three islets west of Shortland (E26) are highly variable. Extreme individuals closely resemble the Shortland race C9 on the one hand and *dahli* E25 on the other, while every degree of intermediacy is found (p. 156).

On San Cristobal C17a also there is considerable variation between males, in the amount of rufous on the breast and of black on the head and tail. Their song, too, is remarkably variable (Cain & Galbraith, 1956). Though the San Cristobal race agrees with the rest of group C in the yellow throat, and the olive cap and pale bill of the female, it differs from the standard pattern of that group in most other characters. It is much smaller. The male has a yellow chin, black tips in the fore-edge of the gorget, a rufous breast-patch, and partly olive head and tail. The female is bright yellow underneath, with a narrow gorget and no melanic wash, lacks rufous on the upperparts (including the wings), and has a partly black tail. Many of these characters of the males are retarded, and of the females advanced.

Avifaunally San Cristobal is distinct from the rest of the Solomons, with several endemic forms showing markedly reduced size (*Collocalia esculenta makirensis, Ptilinopus solomonensis solomonensis, Halcyon chloris solomonis, Rhipidura rufifrons russata, Monarcha vidua, Myiagra cervinicauda* and *Aplonis grandis dichrous*), reduced sexual dimorphism (*Coracina tenuirostris salamonis, C. lineata makirae,*

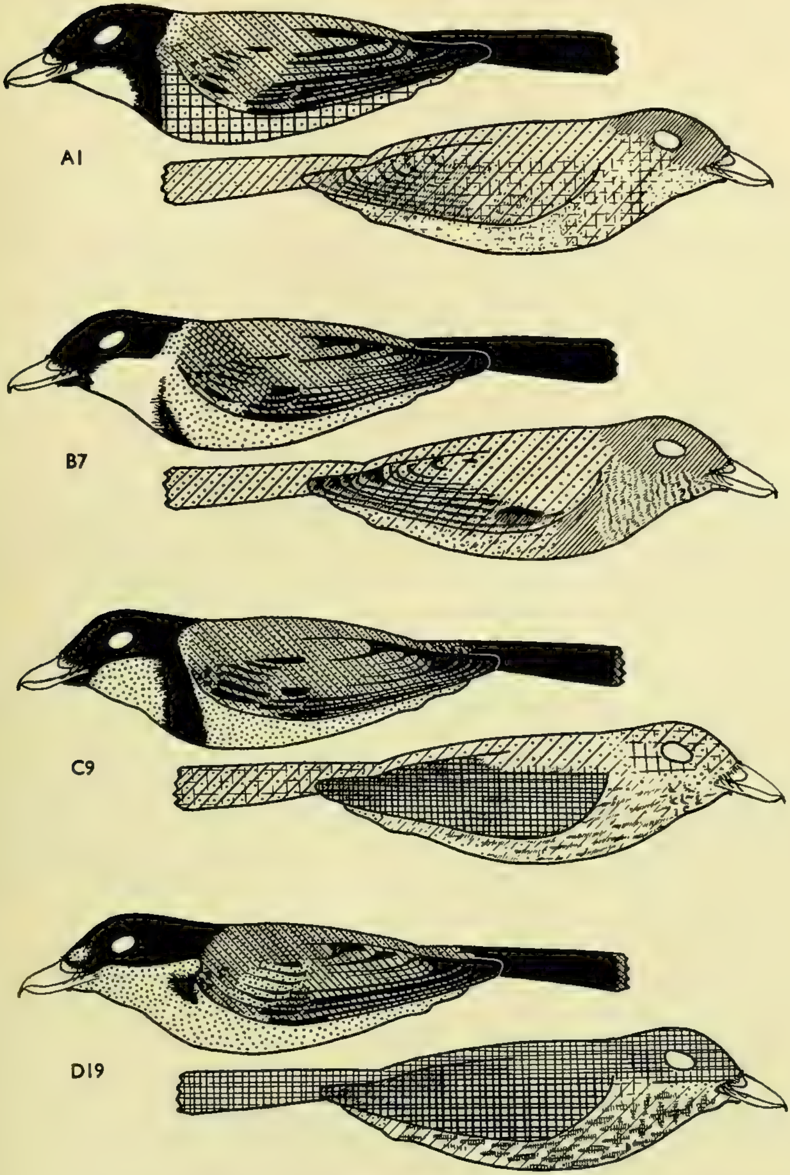

FIG. 2.—Four extreme forms of *P. pectoralis* (*schlegelii* assemblage) which intergrade with more nearly standard ones (*soror* assemblage). Sumba A1; Ternate B7; Shortland C9; Vanua Levu D19a.

Myiagra cervinicauda, *Myzomela nigrita tristrami* and *Dicaeum tristrami*), or increased variability (*Ptilinopus solomonensis solomonensis*, *Halcyon chloris solomonis*, *Coracina lineata makirae* and *Petroica multicolor polymorpha*) in comparison with their western representatives. These trends may result simply from the isolated peripheral position and impoverished avifauna of the island. However, several birds on San Cristobal and its outlying islands are derived from southern Melanesia rather than from the rest of the Solomons (*Ptilinopus richardsii*, *Lalage leucopygia*, *Vitia parens*, *Rhipidura fuliginosa*, *Myiagra cervinicauda* and *Myzomela cardinalis*). The variability of the male of *P. pectoralis* here suggests the possibility of hybridization, which might have disturbed the sexual dimorphism (p. 165). The Vanikoro race G38 shows some of the characters to be expected in the other putative parent : the female is rather similar to that on San Cristobal, except for its streaked white throat, while the juvenile has a streaked but yellow throat. The San Cristobal race shares with most members of group G the pale tail of the male and the melanin-free throat of the female ; and with the New Caledonian race G34 the rufous breast-patch and pale cap. In the light of extensive hybridization between unlike forms elsewhere, it seems most probable that the San Cristobal race is a hybrid between groups C and G.

The New Caledonian race G34 differs from its neighbours of group G in several systematically important characters of the male plumage, which suggest affinities with *P. schlegelii* and groups A to C of *P. pectoralis* (the *schlegelii* assemblage, p. 168). The elongation of the white feathers at the sides of the throat and the failure of the gorget to join the auriculars are reminiscent of group B. The absence of black tips in the fore-edge of the gorget (laterally) is characteristic of the whole assemblage. The rufous breast is found elsewhere only in *P. schlegelii* and group A, and on San Cristobal, and is in the form of a patch rather than a band only on New Caledonia and San Cristobal. These two forms share also the pale cap, and the suppression of the collar (except for lateral patches in the latter). Though the females on these two islands are very different, that on New Caledonia agrees with typical females of group C rather than of group G in having the belly washed with melanins. The number of characters involved makes it improbable that they have been developed independently, and it seems likely that this race too has had genetic contributions from group C as well as group G.

Two further forms, here assigned to group H, show characters which are elsewhere systematically important and confined to the *schlegelii* assemblage (see Table III). The race on the Tenimber Isles H42 has a yellow throat. That on Ndeni and the Santa Cruz islets H52 has overlapping throat feathers without black tips, and a black mantle. But in other respects these forms agree well with members of group H. It would not be justifiable (without further evidence) to deny the possibility of indenpendent origin for these characters, and to postulate mixed ancestry for these forms also. A latent tendency towards yellowing of the throat is apparent in many forms (p. 142). In the melanic race H52 the elongation of the throat feathers and the exclusion of melanin from their tips may be significant in maintaining the conspicuousness of the throat-patch despite encroachment by black areas (as in the other melanic race C13).

The populations between Koro and the large Fijian islands (D18b & 19b–20a) are evidently hybrid (Mayr, 1932b). There is much variability—especially on Ovalau, Rambi and Kio D18b & 19c—in the degree of development of the male gorget and forehead-spots, and in the colour and streakiness of the female underparts. The average character of the populations changes progressively from Koro to the mainland of Vanua Levu (D20b to 19a), while the population on Ovalau D18b is intermediate in character between those of Koro D20b and Vitu Levu D18a. Unfortunately, my material is inadequate to demonstrate quantitatively the changes in hybrid index and in variability which are qualitatively apparent in Mayr's description.

The races on Koro and Vatu vara D20b–21 are themselves intermediate in character between the extreme Fijian forms (D18a & 19a) and members of group H, to which they are linked by the races in southern Fiji H54–56. Males on Koro and Vatu vara have yellow throats with gorgets, those in southern Fiji white throats with gorgets; the yellow forehead reappears on Vatu vara; while all Fijian males have the collar obscure or very narrow. Females in southern and central Fiji (D20–21 & H54–56) are all much alike—differing from those of northern Fiji in having unstreaked cinnamon underparts, and from most of those in group H in having them almost uniform from chin to vent and with scarcely any carotenoid. Blackness of the mantle (D20 & H55–56) and greyness of the wing quills (D19 & 21 & H56) are common to forms on either side of the intergroup boundary.

Group H intergrades with groups A and B also. The male on Sumba A1 has a black chin, a small throat-patch, no black tips in the fore-edge of the gorget, a rufous ventral wash and a wholly black tail. These characters are reduced or absent elsewhere in group A, the dilution being greatest in the Flores Sea A4 and least in Java A2a. Although there is a sharp change in size at the Ombai Strait (along which the boundary between groups A and H has been drawn), and the special male characters of group A do not appear east of it, the female on Timor H39 is very like that in the Flores Sea (which differs from other females of group A in having a pure white throat and pinkish belly), and there is a fairly complete series of forms leading to a typical member of group H on Buru (H39 to 41 & 44).

Males in the northern Moluccas B6–7 have black chins, long throat-feathers partly covering the gorgets, and wholly black tails; while the females are unusual in their heavily-barred throats, pure greys and olives, olive breasts and grey auriculars. There is a perfect series of intermediates leading from these through Obi B8 and Ceram H43 to Buru H44. Although the male characters of group B do not appear there, the female in the Peleng Isles H46 is very like that on Obi B8, and the Sula Isles female H45 is intermediate between those of Peleng and Buru.

The changes involved are quite different in these three areas of intergradation. They involve oddities of pattern, as well as the quantitative changes which seem more likely to be subject to environmental selection. Only in the Lesser Sunda Isles is there a marked climatic gradient (of increasing aridity eastwards from Java to Timor) with which the progressive change in character might be correlated. But here the character-progression (from A1–2a–2b–3–4–H39) does not run parallel to that of climate. In the Moluccas the changes span only seven degrees of latitude across the equator, and in Fiji four degrees within the tropics, so that regular climatic changes cannot be great. It seems unlikely that adaptation to environmental gradients is involved in these character-progressions, although adaptive clines might be developed in relation to subtle differences (perhaps in the fauna or flora). The geographical patterns of character-dilution suggest introgression rather than continued gene-exchange between gradually diverging populations (see Text-fig. 8). Finally, groups A, B and D seem (p. 168) to be more closely related to one another than to group H, with which they all intergrade.

There is thus no reason to believe that the intergradation in these areas is primary. The situation can be explained with the maximum economy of hypothesis in terms of a recent burst of range expansion by group H, which has come into secondary contact with diverse and anciently-isolated forms and freely interbred with them. The same thing has almost certainly happened in the western Solomons, where *dahli* E25 is a relatively very recent arrival and the hybrid population E26 is still exceedingly variable. Meise (1936) and Mayr (1942) have suggested that the *Pachycephala* on Koro D20b is of hybrid origin and has been genetically stabilized by subsequent selection. This seems much the most probable explanation for the other intermediate, though not especially variable, forms just considered.

Since the characters which distinguish groups E to H from one another are relatively slight and mainly quantitative, it is more difficult to decide whether the intergradation between these groups is primary or secondary. On the other hand there is less reason to doubt that the rather similar forms involved can interbreed, and the character-geography strongly suggests gene-flow between these groups in several areas (Text-fig. 8).

Mayr (1954*a*) has pointed out that, while the male in southern New Guinea E24 is like its relatives E23 and 25, the female shows (in its buffy belly with little yellow, and lack of black in the tail) dilution by characters of group F. The dilution appears to decrease into south-eastern New Guinea E26a (Rand, 1940). It is clear that gene-flow from northern Queensland F31b is involved. Mayr also suggests that the character gradient in mid-western Australia (E22d to a) is the result of gene-flow from south-western Australia F28a. The partly olive tail of the male and the reduction of carotenoid support this ; but the birds become smaller southwards instead of larger, and the female shows no sign of the pinkish underparts and barred throat characteristic of the south-western form. It seems more probable that the changes are clinal (p. 187).

In the Louisiades H47, the female shows the bright yellow underparts, white throat (though without mottling) and narrow gorget of group E, but has a very brownish mantle like those of group H, while the male has olive edges to the wing quills. This form could equally well be assigned to either of these groups. The female on Tabar H50 resembles those of group E in the same respects, as to a lesser degree does that on Manus H51. It seems reasonable to suppose that the intergradation in the Louisiades is secondary, and this might be true of the Tabar race also ; but it is most unlikely that the small and recently-arrived populations of *dahli* E25 in the Bismarcks could sufficiently swamp the presumably large population on isolated Manus. This is surely a case of convergence, as in Tonga H57.

While the male on Damar H41 is very like those of Timor and Babar H39–40 (which I suppose to have been affected by gene-flow from group A), the female is different, closely resembling that of the Sula Isles H45 (which has affinities with group B). There may perhaps have been gene-flow across the Banda Sea. But the barred throat characterizing these females is also found in Australia, and the male on Damar has grey edges to the wing quills like those of group E. If gene-flow (other than from group A) is involved here, it seems more likely that it has been across the Timor Sea from northern Australia E23.

The three forms in the Santa Cruz archipelago are remarkably different. The male on Ndeni and the islets H52 is melanic and has the throat feathers elongated, while those on Utupua H53 and Vanikoro G38 are close to the standard. Groups E to H differ mainly in the characters of the female. The Ndeni female is very near the standard, and a typical member of group H ; that on Vanikoro is quite different, most like the Snow Mountain female E27, and apparently a northern representative of group G ; while that on Utupua is intermediate between them. It is possible that this intergradation is primary, and that group H has spread west and east after its origin in the Santa Cruz, but more probably the contact was secondary.

Marks of hybridity

Knowing that hybridization is possible between very dissimilar forms of *P. pectoralis*, we have considered many forms which are intermediate, both geographically and phenotypically, between well-marked groups to be of hybrid origin, even though their variability is not exceptional. Several of these presumably hybrid forms differ from both putative parents (and from most other forms in the superspecies) by characters which are retarded in the male, or advanced in the female plumage. Partly olive (or grey) tails in the male are found in *P. soror* and the southern members of groups E, F and G ; in certain presumptive hybrids (San Cristobal C17, Timor to Damar H39–41, Louisiades H47 and Kandavu H54) ; and nowhere else. Female throats without melanic washes or mottling are found in *P. soror* and the southern members of groups E and G ; in some hybrids (Flores Sea and Salayer A4–5, San Cristobal C17, Timor and Babar H39–40, Louisiades H47 and Utupua H53) ; and nowhere else. Partly black tails in the female are found in *P. soror* and members of group E ; on San Cristobal C17 (and black shafts on Babar H40) ; and nowhere else. The presumptive hybrid females on Obi B8, Babar H40 and Utupua H53 have much brighter yellow bellies than their relatives on either side.

In other parts of the species range, the amount of black in the tails of both sexes, and the depth of carotenoid coloration, are involved in character-progressions which may be climatically determined (p. 186). But while in these clines intensity of pigmentation increases with increasing temperature and humidity, in the forms under discussion the male tail tends to be pale and the female tail and belly to be deeply-coloured. Furthermore, there is no reason to suppose that the islands in the Flores Sea, Timor, Babar, Damar, Obi, the Louisiades, San Cristobal, Utupua and Kandavu share environmental factors which distinguish them from neighbouring islands. If the apparent regularities are real, it seems most probable that they are related to the secondary intergradation which characterizes *P. pectoralis* in these areas.

These trends are not the phenotypic expression of heterosis, since the variable hybrid populations E26, D18b & 19b–c do not show them. Possibly the tendency towards breakdown of the sexual dimorphism reflects genetic disturbances produced by hybridization, or selective changes involved in regaining a balanced genome. These might be expected sometimes to blur the distinction between the adult female and juvenile plumages, producing retarded rather than advanced characters in the female. This may be the explanation for the reversal of south-to-north changes in northern Queensland (p. 156). Many characters might be considered as advanced or retarded, and it would be dangerous to take their occurrence as evidence of hybrid origin ; but the possibility of such effects needs to be considered in assessing the systematic importance of characters, and in tracing environmental correlations.

Though these characters tend to appear together in forms of hybrid origin, the distribution of each is very erratic. The abrupt loss of black from the male tail (coinciding with a sharp increase in size, and the loss of ventral rufous) at the Ombai Strait, and its progressive reappearance eastwards here (H39 to 41) and in the Louisiades (H47a to c) suggests that this character may be dependent upon a rather precise balance between genes from each parental group. If this is true of all the " marks of hybridity ", and each has a different threshold value which depends also upon the parental genomes involved, the sporadic realization of these trends is not surprising.

Sympatry

All the forms of the *pectoralis* superspecies replace one another geographically, except in New Guinea. There *P. soror* and *P. schlegelii* represent one another altitudinally, but meet at about five thousand feet. There is no sign of intergradation between these very distinct species. They are the endemic representatives of *P. pectoralis*, and occupy the primary hill and mountain forest respectively. *P. pectoralis* itself has only been able to enter New Guinea by way of certain disturbed habitats. In the lowlands of the south and south-east E24–25a, it occupies coastal second growth, and may never come in contact with *P. soror* of the hill forest (though they are only three miles apart on Fergusson and Goodenough Islands respectively). Another race of *P. pectoralis* is known only from two river valleys on the northern slopes of the Snow Mountains E27. These valleys have been much affected by intensive native cultivation, which has stripped the forest from their floors and far up their sides. The local race of *P. pectoralis* seems to live largely in second-growth stands of *Casuarina* in the resultant grasslands, but also in the forest (Archbold, Rand & Brass, 1942). *P. schlegelii* descends a little way into the valley forest, and is found there side by side with *P. pectoralis*, with no signs of intergradation. Elsewhere in New Guinea *P. soror* is found up to the level of the valley floors, but it seems to be absent locally, and only appears in the hill forest more than a thousand feet lower.

P. soror and the mountain race of *P. pectoralis* are so much more alike than intergrading forms outside New Guinea that one would expect that they must be conspecific. But the absence of interbreeding between them can scarcely be due solely to extrinsic barriers. They have been collected within a few miles of one another (on the only expedition which has yet encountered the montane race of *P. pectoralis*) and must surely meet on occasion. *P. pectoralis* in the Snow Mountains is separated from its relatives in southern New Guinea by over three hundred miles of primary forest. It seems possible that further investigation will show the known populations to be a few of many, small and scattered among the mountains, wherever disturbance of the forest by man, landslide, wind, flood or fire provides a shifting foothold (cf. Rand, 1941, on the origin of the grassland avifauna). In any case, *P. pectoralis* has presumably passed through the range of *P. soror* to reach the known localities in the Snow Mountains. It is not strictly true to say (Rand, 1940) that this race of *P. pectoralis* shows no closer relationship to *P. soror* than does the southern New Guinea one. Discounting the effects in southern New Guinea E24 of gene-flow from group F, most of the changes (male throat feathers grey-based, collar reduced, mantle greener, edges of wing-quills olive and broader, female with olivaceous breast, brown cap and blacker tail) are in fact in the direction of *P. soror*. But even if these differences

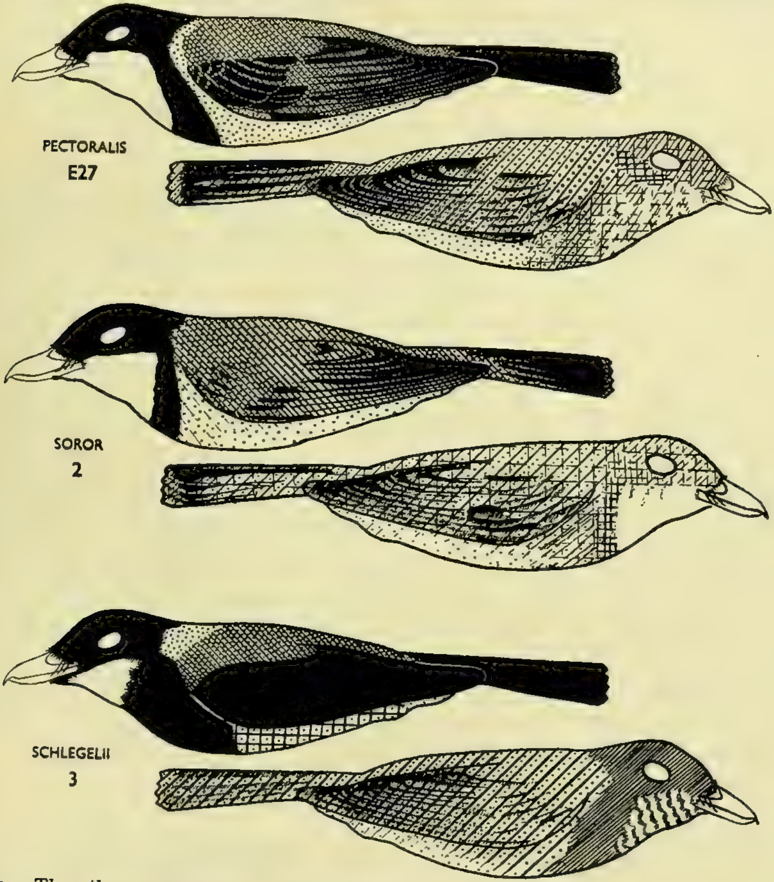

Fig. 3.—The three sympatric forms, in the Snow Mountains of New Guinea. *P. pectoralis* E27; *P. soror* 2a; *P. schlegelii* 3a.

from other members of group E imply gene-flow from *P. soror*, rather than parallel adaptation to higher altitudes (p. 188), the introgression must have been slight and soon ended. The great reservoir of *soror* genes would otherwise soon swamp the small populations of *P. pectoralis* in the mountains, destroying not only the rather slight phenotypic differences but the genetic determination of habitat preference which presumably keeps the two forms apart. Although the evidence is very indirect, it seems that *P. soror* and group E of *P. pectoralis* are genetically sympatric species.

A rather similar situation arises in the Bismarcks, where *dahli* E25 occupies small islands (but also occurs at certain coastal localities on the large islands) while the endemic race H48 keeps strictly to the dense forest inland (Dahl, 1899). Probably because of this difference in habitat preference, there seems to be little interbreeding between the two forms, though Hartert (1926) records that occasional males on New Britain combine the smaller size and greener mantles of the endemic race with the greyer wings of *dahli*, and Mayr (1955) suggests that much of the internal variation of *dahli* may be the result of gene-flow from group H. The two forms must meet occasionally, though *dahli* may not normally breed on the large islands. It would be reasonable to suppose that groups E and H must be partly isolated by intrinsic barriers, like *P. soror* and the Snow Mountains race of *P. pectoralis*. Yet in the Louisiades H47 the same groups have merged completely.

Several explanations might be put forward to account for this anomaly, any or all of which may be true in part. It may be that in the Louisiades existing barriers have been broken down by hybridization (cf. Sibley, 1954*b*), permitting the populations to merge, while *dahli* has not been long enough in the Bismarcks for this to have happened. Or the populations of group H endemic on the relatively small islands of the Louisiades may have been inadequately shielded from interbreeding by differences in habitat-preference. Or after interbreeding in the Louisiades, *dahli* in the islands west of the Louisiades (E25b–c) may have secondarily developed barriers against group H, before invading the Bismarcks. In the absence of positive evidence, it is safest to assume that the two stocks in the Bismarcks represent one another geographically, and seldom meet in the breeding season. Yet it is conceivable that intrinsic barriers to interbreeding are effective here. From this, and from the different reactions of the *schlegelii* and *soror* assemblages (and of differentiated stocks within the latter) when they meet in New Guinea and in the archipelagos, it is clear that species-limits need not at all closely follow the pattern of descent and resemblance.

P. schlegelii, *P. soror* and group E of *P. pectoralis* are genetically sympatric (Cain, 1953) and must be regarded as good species. Yet the subspecies-groups A to H of *P. pectoralis*, some of them much less alike than are *P. soror* and group E, are interconnected by a web of secondary intergradation (Text-fig. 4). In the absence of evidence that groups E and H meet in the breeding season without significant interbreeding, all these groups can be included in a single species.

GROUP AFFINITIES

The ***schlegelii*** assemblage

P. schlegelii, groups A to D of *P. pectoralis*, and *P. flavifrons* all differ markedly from the standard patterns for the superspecies. Each is distinguished from the others by characters which are not merely striking but stable and systematically important (as is shown by their co-variation). At first sight they seem to be independently derived from more standard forms, rather than closely related to one another. There is little in common, for example, between *P. schlegelii* and the Fijian group D (Text-figs. 3 and 2, bottom).

Yet there are important resemblances between members of this assemblage of forms. Most striking is the similarity between females of *P. schlegelii* and of *P.*

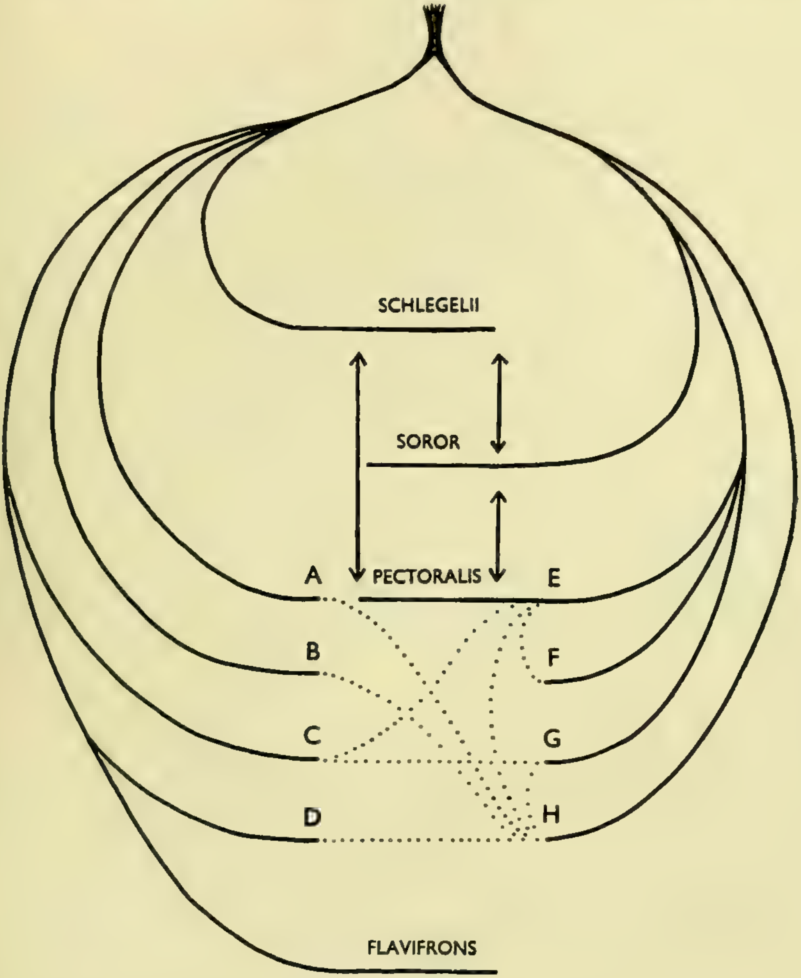

FIG. 4.—Diagram of the phylogeny suggested for the superspecies, showing secondary intergradation between subspecies-groups of *P. pectoralis* (dotted) and sympatric co-existence in New Guinea (arrows).

pectoralis in the northern Moluccas (group B). Furthermore, the males of the same forms are alike in having black chins, and throat-patches overlapping the gorgets without black tips to the feathers. These two characters of the males are shared by forms in most of the groups of the *schlegelii* assemblage. The black chin is absent from all the hybrid forms and from group D, but characterizes *P. schlegelii*, *P. flavifrons* and undiluted members of groups A to C. It is not found elsewhere in the superspecies (except in the black-throated race H57). The unusual structure of the gorget-edge is less affected by gene-flow, and is found in almost all the members of the assemblage which have gorgets. Elsewhere it occurs only on New Caledonia G34 (possibly related to the assemblage) and Ndeni H52 (see p. 162).

Several other characters serve to link two or more groups. In this way each of the groups is united with at least one other: groups A to C of *P. pectoralis* to one another and to *P. schlegelii*, group D to group C, and *P. flavifrons* to group D. Table III sets out the main characters which occur in more than one group of the assemblage, while remaining rare elsewhere in the superspecies. The table does not illustrate the resemblance between females of *P. schlegelii* and of group B, since this depends on the conjunction of several characters (grey-barred throat, olive breast, grey auriculars and lack of phaeomelanins) which occur separately in several different forms outside the assemblage.

TABLE III.—*Characters Uniting the* schlegelii *Assemblage.*

	schlegelii assemblage						*soror* assemblage
	schlegelii	A	B	C	D	*flavifrons*	
Male:							
Chin black	1–3	1	6–7	9–15	—	×	—
Throat yellow	—	—	—	9–17 (E26)	18–21	×	H42
No gorget	—	—	—	12	18–19	×	—
gorget edge	1–3	1–3	6–8 (H43)	9–11, 13–15	—	—	H52
breast rufous	1–3	1–4	—	17 (G34)	—	—	—
Forehead yellow	—	—	—	—	18–19, 21	×	—
Mantle melanic	—	4	—	13–14	20 (H55–56)	×	H52
Wing black	1–3	4	—	13–14	—	×	—
Tail black	1–3	1	6–7	13	—	×	H52
Female:							
Cheeks yellowish	—	—	—	9, 11 & 12	18–19	—	—
Underparts streaked	—	—	—	9–16	18–19	—	—
Wing russet	—	—	—	9–16	18–21	—	—

The ***soror*** assemblage

P. soror and the remaining groups of *P. pectoralis* are united negatively rather than positively, by the absence of those unusual characters which distinguish and link together the groups and species belonging to the *schlegelii* assemblage. Since group H as a whole scarcely departs from the average characters of the whole superspecies, it can be associated with other groups only negatively. However, there are a few characters and trends which link *P. soror* with groups E to G and these with one another, and are rather rare in the *schlegelii* assemblage. These are set out in Table IV.

TABLE IV.—*Characters Uniting the* soror *Assemblage (except Subspecies-group H).*

	soror assemblage				
	soror	E	F	G	*schlegelii* assemblage
Male:					
Carotenoid pale	1–3	22	28–30	34, 36–38	—
Quills grey	1–3	22–25	28–30	—	D19, 21
Coverts yellow	—	22–25	28–32	35	D18–19
Tail pale	1–3	22	28–32	34–37	C17
Female:					
Throat white	1–3	22–27	—	34–38	A4–5
Throat streaked (not belly)	—	25, 27	—	38	—
Cap grey (not auriculars)	—	22–25	28–33	—	A5

Several of these characters seem to appear chiefly in higher latitudes, and may be related to the generally cooler climates encountered by these groups. Yet they are very different from the characters of *P. schlegelii*, which lives at higher altitudes than *P. soror*. The resemblances between group F and the Vanua Levuan race D19 (grey-edged wings and yellow-edged wing-coverts in the male; barred throat, melanic belly and almost complete absence of carotenoid in the female) may be due partly to selection under cooler climates. These characters, and others which (it may be objected) could be used to erect any number of alternative assemblages, are evidently unstable, since they appear independently in widely-scattered localities and cut across the discontinuities indicated by the co-variation of more stable characters.

ARRANGEMENT

The considerations of relationship, intergradation and sympatry discussed above permit the various forms to be arranged systematically. The categories of superspecies, species, subspecies-group and subspecies are used, and considerable infra-subspecific geographical variation is recognized.

The superspecies

The category of Artenkreis or superspecies (Rensch, 1928; Mayr, 1931*a*) was introduced for groups of strictly allopatric representatives, some of which are too unlike to be considered conspecific. Mayr pointed out that the great practical usefulness of this category might be expected to decline as the possibility of unlike representatives being conspecific became generally accepted. More recently the scope of the superspecies has been extended to include groups of forms some of which are genetically sympatric (Cain, 1953), with their breeding ranges even overlapping slightly (Mayr and Vaurie, 1948 ; Mayr, 1949 ; and definition in Mayr, Linsley and Usinger, 1953). This extension gives the category permanent value, in expressing the relationship between forms which can never be considered conspecific yet which have barely ceased to represent one another geographically. But it removes the objective criterion which limited the use of the superspecies under the older usage, and opens the way to further extension. There is a danger of the category losing its special connotations of geographical replacement, becoming synonymous with the species-group.

Sometimes a species or superspecies is represented locally by a pair of sympatric species, so that it would be arbitrary to include one rather than the other in the superspecies, or to exclude both. Cain (1954*b*) has introduced the term " doublet " for such pairs in the *Ptilinopus purpuratus* superspecies, and this usage is helpful in indicating cases of double invasion. Where triple invasion by a single species has resulted in three representatives locally, the term " triplet " may be used. For example, *Zosterops lateralis* is represented by a doublet on Lord Howe (*Z. strenua* and *Z. l. tephropleura*), and by a triplet on Norfolk Island (*Z. albogularis*, *Z. tenuirostris* and *Z. l. norfolciensis*).

P. soror is so like many members of *P. pectoralis*, while *P. schlegelii* is so strikingly different, that the former is the obvious New Guinea representative. *P. soror* and *P. pectoralis* seem to be only genetically sympatric, without actual overlap, and might be included in one superspecies. But we have seen that, while *P. soror* is indeed the more closely related to some subspecies-groups of *P. pectoralis*, *P. schlegelii* is so to others. The two species should therefore be considered as a New Guinea doublet, like *Ptilinopus coronulatus* and *Pt. pulchellus* (Cain, 1954*b*). The local intrusion of *P. pectoralis* itself means that there is a triplet on the northern slopes of the Snow Mountains.

Species

All the remaining forms are geographical representatives. Those that intergrade must be conspecific, so that even the extreme forms on Sumba and in the northern Moluccas, Solomons and northern Fiji belong to *P. pectoralis*. Certain striking single characters have evidently arisen several times independently, and most modern systematists would agree in placing within *P. pectoralis* both the hen-feathered races on Rennell and Norfolk Island C16 & F33, and the melanic ones in the Solomons and Santa Cruz C13 & H52.

However, there are a few extreme forms (Text-fig. 5) whose status is doubtful, and can only be decided by comparing the degree of difference between them and their nearest relatives with that shown between sympatric species on the one hand, and between intergrading subspecies on the other. But in the *pectoralis* superspecies, two sympatric forms are much more alike than many intergrading ones : the relationship between visible differentiation and the establishment of barriers to interbreeding is not the same in New Guinea as in the archipelagos. The forms of doubtful status are all found on more or less isolated islands, whose avifaunas are much poorer in species than those of New Guinea and include at most one other species of *Pachycephala* (*P. rufiventris* on New Caledonia). It is reasonable to suppose that the intergradation of unlike subspecies in the archipelagos is more relevant here than the coexistence of like species in New Guinea (p. 179).

P. flavifrons in Samoa is a derivative of the Fijian group D (Table III), but deserves the specific rank always accorded it. Group D is itself the most aberrant in *P. pectoralis*, and is probably on the borderline of ethological and genetic incompatibility with the rest of the species, while *P. flavifrons* has acquired further unusual characters —including the unique cock-feathering of its females.

Previous authors have considered the Tongan form H57 as a distinct species (*P. melanops*) because of the black throat of the male. In other ways this form is

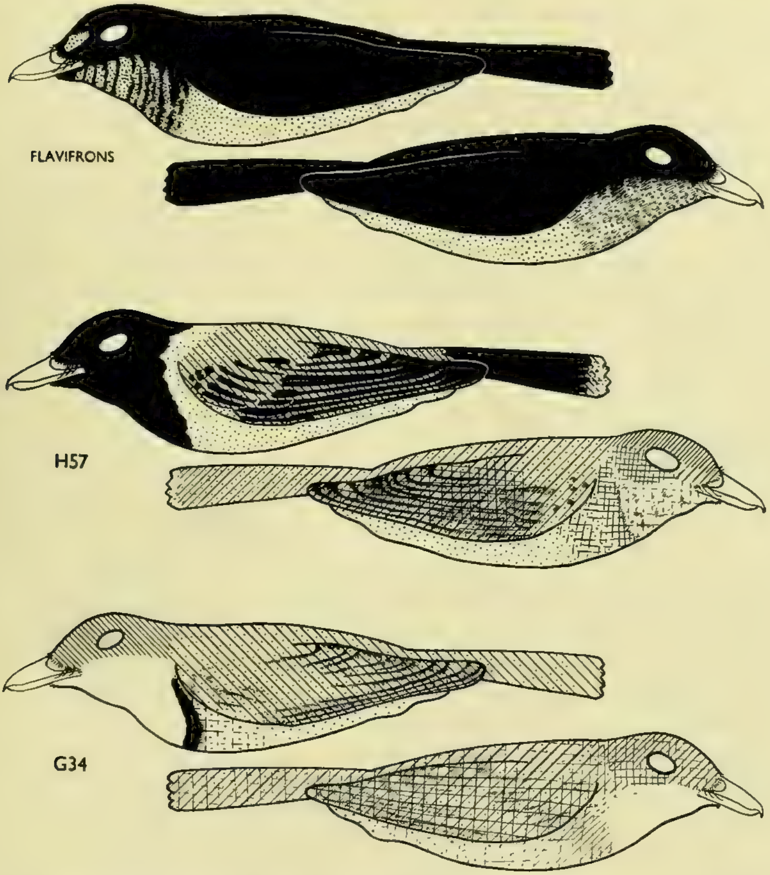

FIG. 5. Three unusual island forms. Samoa, *P. flavifrons*; Tonga, *P. p. melanops* H57; New Caledonia *P.* [*p.*] *caledonica* G34.

rather close to the standard pattern. It seems to be a member of group H, not more modified than might be expected from its isolation and the poverty of the avifauna in which it is placed. There is no reason to believe that the black throat reflects any very profound genetic change. The white throat-patch is very restricted on Sumba A1 and in *P. schlegelii*, and reduced to narrow white barring on black in individuals of the latter's close relative *P. aurea*. The mountain species *P. nudigula* and *P. implicata* (derived from the *pectoralis* superspecies) have acquired blackish throats independently. On the other hand, the black throat does alter the appearance of the male most markedly, and might therefore be of ethological importance. But so does the abolition of the gorget, and even more the total loss of the distinctive male pattern : yet there has been gene-flow between races with and without gorgets, while hen-feathered males in dimorphic races are able to find mates and breed. It is most improbable that the black throat alone would be sufficient to restrict interbreeding while further barriers were selected for, in the event of a second invasion of Tonga. " *P. melanops* " ought therefore to be considered as a race of *P. pectoralis*.

In the New Caledonian representative G34 also the male is unusual, the female less so. The male shows several unusual characters (long throat-feathers, rufous breast-patch and pale cap), which appear independently in other races. This form has been excluded from *P. pectoralis*, even by Mayr (1945), for nomenclatural reasons. *Muscicapa caledonica* Gmelin, 1789—the valid name for it—antedates *M. pectoralis* Latham, 1801, so that merging them should mean changing the well-known name *Pachycephala pectoralis* to *P. caledonica* throughout its seventy-odd subspecies. It would be most undesirable to upset an established name in this way on the basis of a subjective decision. Yet it is also unsatisfactory to recognize the New Caledonian form, considerably less aberrant than the Fijian races, as a distinct species. Mayr (1941*b* and 1945) does not include *P. caledonica* in lists of the endemic species of New Caledonia. Since stability could be maintained by refusing to recognize the subspecific status of *caledonica*, this is not a case which can be submitted to the International Commission for Zoological Nomenclature. I have avoided the dilemma by including *caledonica* among the subspecies of *P. pectoralis*, while enclosing the specific name in square brackets (*Pachycephala* [*pectoralis*] *caledonica*), an expedient suggested by Dr. A. J. Cain.

The third form here included in *P. pectoralis* for the first time is the hen-feathered one on Salayer A5 (*teysmanni*). This has previously been considered as the representative, not of *P. pectoralis*, but of the hen-feathered species *P. orpheus*, which is very like females of group A. It agrees with the former species in its long bill, black in both sexes, and with the latter in its juvenile plumage (streaked below and without rufous on the wings), while it is intermediate in degree of dimorphism. Juveniles of the Sundan group A have less rufous wings than most in *P. pectoralis*, and a nestling from Pantar A3b is greyish with ventral streaking. *P. orpheus* occupies Timor and islands to the east, and it seems on the whole more probable that this and the Salayer form are independently derived from group A of *P. pectoralis*, than that *P. orpheus* has colonized Salayer across the three-hundred-mile gap occupied by *P. pectoralis*, and there partly reversed its loss of dimorphism. If this interpretation is correct, there is no reason to separate the Salayer *Pachycephala* from *P. pectoralis*.

Subspecies-groups

There is no formal category between the species and the subspecies, and I call the eight divisions of *P. pectoralis* subspecies-groups. Zeuner (1943) has used the term in a rather different sense. The recognition of subspecies-groups permits the inclusion of well-marked geographical representatives (e.g. *Corvus corone* and *C. cornix* : cf. Huxley, 1942, 249) in a single species, while still expressing both the distinction between them and the minor subspeciation within each. There are no nomenclatural rules for such informal categories, and it is convenient here to use geographical designations rather than subspecies names for them.

Subspecies

No two populations have precisely the same distributions of genes, so that it is futile to attempt the subspecific separation of all local forms which differ statistically from the others. In avian systematics, some variant of the " seventy-five per cent rule " (see Mayr, Linsley and Usinger, 1953) is widely accepted as a lower limit for the constancy of differences between subspecies. This is a useful check on excessive splitting which should probably be retained whatever further considerations are introduced. But it does not take account of the magnitude and systematic importance of the differences. A very slight though constant difference in a single character which varies in response to climatic differences suffices to separate two forms ; while greater though rather less constant differences in several characters whose co-variation shows them to be largely independent of climate, and of systematic importance, do not. The subspecies-concept remains purely morphological, while that of the species now depends ultimately upon genetic isolation.

In parts of the range of *P. pectoralis*, the birds from almost every island can be distinguished by careful comparison of long series. This is true especially of the New Hebrides (G36–37f) and the Bismarcks (E25d–j and H48a–49). Mayr (1945) recognized six subspecies in the New Hebrides, but now considers that most of these should be combined (*in litt.*). The differences (almost entirely confined to the females) are slight, concern highly labile characters (such as the intensity of carotenoid and degree of phaeomelanization), intergrade through series of islands, and are exceeded by individual differences. The recognition of six subspecies conceals the true situation —that *P. pectoralis* is remarkably uniform throughout a great number of widely separated islands in the New Hebrides, though the population on Aneitum G36 is clearly distinguishable from the rest. I have therefore combined all the remaining populations (G37). The Erromango population G37a deserves subspecific separation according to current usage (p. 205), but those from Efate to the Banks Islands G37b–f should be combined.

Populations of groups E and H are distinguishable in series from island to island in the Bismarcks. The differences in group E are mainly in size, with populations of larger (E25b, c & d) and smaller (E25e) birds distributed apparently sporadically (cf. *Cacatua galerita triton*, Mayr, 1937). There are also slight differences in the pigmentation of the females and in the depth of carotenoid in the males. The situation is best expressed by combining the populations from south-eastern New

Guinea to Nissan E25a–k in *dahli*—though that on Fergusson E25c is on the borderline of subspecific recognition by current usage. There is little greater variation in plumage between populations of group H in the Bismarcks H48a–49, and that little is almost entirely confined to the females. There has as yet been no attempt to divide the populations from Umboi to Lavongai H48a–c, although the females can be distinguished in series (Mayr, *in litt.*). Females on Mussau and Lihir H48d–49 are more distinct—about as much so in relation to the other Bismarcks females as those on Erromango are in the New Hebrides. The Lihir form H49 is here separated subspecifically on account of its much greater size. But while that on Mussau H48d deserves separation under current usage, it is here combined with H48a–c to emphasize the homogeneity of this series of populations in contrast to those of Tabar and Manus H50–51, whose females are much more distinct.

By considering these areas of incipient subspeciation, and raising the level of difference required for separation so as to clarify the pattern of variation, we have arrived at a pragmatic standard for the subspecies of *P. pectoralis*. When this is applied elsewhere in the species range, a number of named subspecies are combined with others. This is especially true of the "small-island forms" (p. 188), of which only those on Ternate and Tidore B7 and Lihir H49 are sufficiently distinct to be separated on size alone, at this level of difference. Some of the remainder (e.g. H43b) are distinct enough for separation according to the seventy-five per cent rule, while others (e.g. A3b) are perhaps not.

The principle that minor subspecies should be combined, in order to emphasize the more important discontinuities, can be applied to variation on continents also. In Australia I have recognized only those forms considered by Mayr (1954*a*) to be original isolates—the subsequent expansion, intergradation and minor evolution of which have partly obscured the situation. Although the mangrove-living forms E22 in north-western Australia are known only from a few widely-separated localities, their variation is wholly of clinal type. The situation could be expressed in nomenclature as "*P. p.* cl. *bynoei-melanura-violetae*" (E22a–c–23), but it is convenient to separate the populations which show these regular changes from the more constant ones to the east E23. In *P. schlegelii* the populations of south-eastern New Guinea 3b should be combined with those of the Snow Mountains 3a, because the changes are slight in comparison with those which distinguish the Vogelkop and Cyclops Mountain races A1–2, and intergrade through central New Guinea (Mayr & Gilliard, 1954). In *P. soror*, on the other hand, there is a sharp change in the colour of the male tail in passing from the Bismarck and Saruwaged Mountains 2b to those of south-eastern New Guinea 3—relatively important in this less variable species.

The populations between Koro D20b on the one hand, and Viti Levu and Vanua Levu D18a & 19a on the other, are variable, and their hybrid indices evidently depend mainly on their distances from the parental populations. That on Taviuni D20a is only slightly affected by gene-flow from Vanua Levu, and is best included with the Koro race. Those on Ovalau D18b and Rambi and Kio D19c are also perhaps closer to the latter, but are considerably modified by gene-flow from Viti Levu and Vanua Levu respectively, and are therefore included in the subspecies of those islands. It does not seem desirable to recognize several hybrid races, differing only in hybrid index and variability (cf. Mayr, 1932b). If this were done, consistency would demand the recognition of the constant Santa Anna population C17b as subspecifically distinct from the variable ones on San Cristobal C17a.

The subspecies numbered on Text-fig. 6, in the check-list, and in the text are delimited to make as clear as possible the pattern of isolation in the superspecies. It is not suggested that this arrangement should be generally adopted, since it does not accord with current usage, and a list of the subspecies to be recognized is therefore given on p. 205. But it does reveal the more important discontinuities which excessive splitting obscures, and the subspecies thus delimited have perhaps more biological significance, since some attempt has been made to consider discontinuity rather than mere constancy of difference (cf. Sibley, 1954*a*). It seems that the subspecies-concept might with advantage be modified by introducing such considerations. This would seldom require such considerable changes in the number and scope of subspecies as are necessary in the exceptionally variable species *P. pectoralis*.

EVOLUTION

Geographical speciation in New Guinea

The distribution of species and subspecies in many New Guinea birds strongly suggests that northern New Guinea was once isolated (Mayr & Gilliard, 1952), and this agrees with what is known of the tectonic history of the island (Carey, 1938). Some of the northern endemics have since spread into the Vogelkop. The pattern of variation of *P. schlegelii* and *P. soror* and the distribution of forms related to them (discussed below) suggest that they were originally geographical representatives, with the former in the Vogelkop and northern New Guinea (*P. schlegelii* 1–2) and the latter in the rest of the island (*P. soror* 2–3).

P. schlegelii has three distinct subspecies, with that of the Cyclops Mountains 2 combining characters shown by those of the Vogelkop 1 and the Snow Mountains 3 (and so perhaps ancestral to both). The Vogelkop form has invaded the Wandammen Mountains, which suggests that the species was absent from the nearer Snow Mountains at the time of colonization. There is no sharp break between the Snow Mountains 3a and the south-east 3b (though there are gradual clines), suggesting a rather recent expansion in this area. In *P. soror*, despite its greater overall homogeneity, there is a slight but definite break at this point (subspecies 2/3), while there is no appreciable difference between the birds of the Snow Mountains and of the north. This species has evidently colonized the northern mountains much more recently than those of the south-east. Both species have distinctly brown females in the Vogelkop, but in *P. soror* this is the only marked character of the Vogelkop race. Several birds are blacker in the Vogelkop than elsewhere in New Guinea, and this may be related to greater humidity (Cain, personal communication). If the parallel tendencies towards brownness in *Pachycephala* females here are adaptive, the changes may have been produced rather quickly. Also, isolation allows rapid change, unimpeded by gene-flow. *P. soror* may have been longer in the south-east than in the Vogelkop, despite the greater distinctiveness of the female in the latter area.

Two species in New Guinea seem to be hen-feathered derivatives of *P. schlegelii* and *P. soror*. *P. lorentzi* is found within the geographical and altitudinal range of *P. schlegelii* in the Snow Mountains 3, and resembles the female of that species. *P. meyeri* bears the same relationship to *P. soror* in the Vogelkop 1. If these are relicts of early reciprocal invasions, their distribution tends to confirm that at one time *P. schlegelii* was absent from the Snow Mountains, and *P. soror* from the Vogelkop. Distribution and variation within *P. pectoralis* further reinforce this suggestion. Females of the Moluccan subspecies-group B, geographically near the Vogelkop, are remarkably like those of *P. schlegelii* (p. 169). Central members (subspecies-groups A to C) of the *schlegelii* assemblage are distributed towards the north of the species range, while the *soror* assemblage (especially the central groups E to G) is southerly. The early distribution of the assemblages according to this hypothesis is shown in Text-fig. 7, from which group H is omitted because its origins are obscure (p. 182).

Origin of the dichotomy

The presence of a doublet, representing locally a single more widespread species, implies double invasion. It has been suggested above that in the *pectoralis* superspecies the second invasion took place within what is now New Guinea. If this is not true, the evidence suggests that *P. schlegelii* represents the endemic New Guinea stock, and that the *soror* stock arose as its geographical representative in Australia. While (outside New Guinea) the *schlegelii* assemblage is confined to islands, the *soror* assemblage occupies Australia. It must be rare for a form evolved in isolation on an archipelago, in competition with relatively few species, to compete successfully in the rich avifauna of primary forest on a continent, especially under the different physical conditions at high altitudes. But an Australian forest bird might well colonize the New Guinea hill forest. Gradual invasion across the Arafura shelf (often dry in the past) might favour the perfection of predeveloped isolating mechanisms (p. 180). The scattered and restricted subspecies-groups belonging to the *schlegelii* assemblage show a relict distribution comparable to that of the old species in the *Rhipidura rufifrons* superspecies (Mayr & Moynihan, 1946), while the *soror* assemblage occupies a wide and almost continuous range, like that of *R. rufifrons* itself, most of which has evidently been colonized comparatively recently. Patterns of intergradation in *P. pectoralis*, especially in the Banda Sea, suggest that the *soror* assemblage is still expanding (presumably as the result of selection) at the expense of the *schlegelii* assemblage. It is hard to accept the latter as a relatively recent colonist of New Guinea, in the face of competition from an entrenched *P. soror*.

Since the intergradations of group C with the *soror* assemblage are evidently secondary (p. 160), it is necessary to pass through group H in order to derive *P. soror* from proto-*schlegelii* by way of primary intergradation in the archipelagos (see Text-fig. 7, right-hand inset of Text-fig. 6, and Text-fig. 8). Of the possible sequences by which it could be derived in this way, the least improbable is *schlegelii*–B–H–G–E+F—*soror* ; but it is not convincing. The almost inescapable conclusion is that the *schlegelii* stock arose from the common ancestor in New Guinea, and the *soror* stock either there or in Australia. This implies that *P. schlegelii* and *P. soror* are not merely terminal forms without issue, such as are produced by the double invasion of islands (e.g. *Zosterops*, p. 172 ; *Ptilinopus mercieri* and *Pt. dupetithouarsii*, Cain, 1954*b*), but represent the basal forms of their respective assemblages, geographically very near to their areas of origin.

Since the sympatric species *P. schlegelii* and *P. soror* are connected by way of secondary intergradation in *P. pectoralis*, which proves to be specifically distinct from them both, this conclusion seems to imply reticulate evolution (Text-fig. 4). The origin of a genetically isolated new species from two existing ones is a commonplace in botanical systematics, but the mechanism commonly involved (allotetraploidy) seems to be incompatible with the genetic mechanisms of sexually-reproducing animals (see Dobzhansky, 1937). There is no question of any such mechanism being involved in the *pectoralis* superspecies, since the forms of *P. pectoralis* which are in the biospecific relationship to *P. soror* (E24 & 27) are pure members of the *soror* assemblage. However, the evolution of the superspecies appears to have been reticulate at the species level only if the present status of *P. schlegelii* and *P. soror* is conventionally reflected back in time to their point of divergence. At the time when gene-flow between proto-*schlegelii* and proto-*soror* effectively ceased, permitting them to diverge in isolation, the barriers between them were probably almost entirely extrinsic ; and there is no reason to suppose that intrinsic isolating mechanisms had been perfected before they independently colonized the archipelagos and Australia. The existing mechanisms are local products of selection, and the supposition that the primary dichotomy of the superspecies took place in New Guinea does not imply that established species barriers were later broken down.

Development of isolating mechanisms

While in New Guinea the *schlegelii* and *soror* assemblages are represented by distinct biospecies, in the archipelagos they have proved capable of interbreeding freely wherever they have met. Biologically, New Guinea is strikingly distinguished from the surrounding islands by its vastly richer fauna. It is the centre of distribution of *Pachycephala*, with twelve species (cf. Mayr, 1941*a*—*P. aurea*, *P. lorentzi*, *P. meyeri*, *P. simplex* (with *griseiceps*), *P. hyperythra*, *P. modesta*, *P. rufiventris* (with *monacha*), *P. rufinucha*, *P. tenebrosa*, and the *pectoralis* superspecies). At the time when *schlegelii* and *soror* were developing intrinsic barriers against interbreeding with one another, they were probably in effective contact with most of the other nine. It may well be that the barriers were to some extent predeveloped before the two stocks met again, as a by-product of selection acting towards isolation from their sympatric congeners (especially *P. meyeri* and *P. lorentzi*). Similarly, *P. soror's* barriers against the closely related subspecies-group E of *P. pectoralis* may have been prospectively developed, when the former came in contact with *P. schlegelii*.

In Australia, *P. pectoralis* is in effective contact with *P. simplex*, *P. rufiventris*, *P. lanioides* and *P. olivacea* (of which the first two are probably rather recent arrivals

—Mayr, 1954*a*). Possibly the specific distinctness of group E from *P. soror* is partly related to the development of barriers against these, and especially against the northern mangrove species *P. lanioides* and *P. simplex.*

In the archipelagos *P. pectoralis* meets with no more than one congener on any island: with *P. grisola* on Java and Bali (A2); with *P. nudigula* on Sumbawa and Flores (A3a); with *P. orpheus* on Timor and Wetar (H39); with *P. rufiventris* (including the *griseonota* group) on Damar, Tenimber, the Moluccas and Sula Isles, Rossel and New Caledonia (H41–45, B6–8, H47c & G34); with *P. simplex* on Fergusson (E25c); and with *P. implicata* on Bougainville and Guadalcanal (C9 & 11). Of these *P. grisola* in the lowlands, and *P. nudigula* and *P. implicata* in the mountains, are altitudinally separated from *P. pectoralis,* while *P. rufiventris* probably occupies drier habitats on the average (as in Australia) and shows altitudinal separation on Ceram and Buru (pp. 189–190). Only on Timor and Wetar is there an overlap, of long standing and without marked ecological separation, between *P. pectoralis* and a closely-related species, *P. orpheus.* On Timor and Wetar, *P. pectoralis* is large in comparison with its relatives to the west, and with sympatric *P. orpheus*; which in turn has large representatives (*par*) on Roma, Letti and Moa, where the former does not occur. This suggests that there has been selection for size difference between the two species in the zone of overlap, as between *Sitta neumayer* and *S. tephronota* (Vaurie, 1950). It is noteworthy that in this region the intergradation between subspecies-groups of *P. pectoralis* is strongly stepped at the Ombai Strait (between subspecies-groups A and H), which suggests that gene-flow has not been as free as in the Moluccas and Fiji.

It seems therefore that the predevelopment of isolating mechanisms between the *schlegelii* and *soror* assemblages may be related to the intensity of selection against interbreeding with related species, to which the populations concerned were subject before they met. The degree to which they had developed different ecological preferences may also be relevant. It is probably more than a coincidence that group E of *P. pectoralis,* which is genetically isolated from its close relative *P. soror* in New Guinea (and to some extent from group H in the Bismarcks), is the most ecologically specialized in the superspecies (p. 190). New Guinea provides greater opportunities for altitudinal separation than any of the surrounding islands, and *P. schlegelii* and *P. soror* replace one another in this way to an extent seen in the archipelagos between *P. pectoralis* and much less closely related species.

Another factor which may have affected the reaction of the two stocks on meeting is the manner in which this took place. Within New Guinea they would at first have been opposed to one another over a broad front, and separated by the relatively unsuitable habitat of lowland forest. Invasion through this would be slight but continuous, producing rare hybrids in the lowland zone. These would be at a selective disadvantage, and at the edge of this zone there would be strong selection in favour of isolating mechanisms. Once developed these would allow the stocks to overlap, and the developed mechanisms would spread back into the populations, followed by waves of reciprocal invasion. The same would happen where group E of *P. pectoralis* met *P. soror* at the edge of its range, and the development of isolating mechanisms would finally permit the former to penetrate the range of the latter as a distinct biospecies. In the archipelagos, on the other hand, the second colonizing wave (represented largely by group H) would have arrived over water, and its genetic representation in the population would probably be increased less by repeated invasion than by selection. In the absence of effective pre-established isolating mechanisms the new element would be incorporated in the endemic population, and no barriers could subsequently be developed.

A suggested course of events

Several alternative sequences of invasion and differentiation might be suggested, any of which could have produced the existing pattern of variation. It would not be profitable to discuss at length the pros and cons of these hypothetical alternatives, since the evidence does not seem adequate to decide between them with any finality. However, the following sequence seems to fit the facts more neatly than any alternative, and is perhaps worth putting forward for comparison with those deduced for other groups in the area (e.g. *Ptilinopus purpuratus* species-group in Ripley & Birkhead, 1942; *Halcyon chloris* species-group in Mayr, 1949; *Coracina* species-groups in Ripley, 1941, and Voous & van Marle, 1949; *Rhipidura rufifrons* species-group in Mayr & Moynihan, 1946; *Dicrurus hottentottus* superspecies in Mayr & Vaurie, 1948; *Dicaeum cruentatum-hirundinaceum* species-group in Mayr & Amadon, 1947). It is presented without qualification, for the sake of brevity.

It seems that the common stock of the superspecies arose in New Guinea (where the greatest concentration of *Pachycephala* species is to be found at present). *P. nudigula* on Sumbawa and Flores and *P. implicata* on Bougainville and Guadalcanal probably represent the relicts of an early burst of colonization westwards and eastwards respectively. The north-western and south-eastern populations in New Guinea, more or less effectively isolated from one another, diverged as subspecies. From the west and north " *schlegelii* " colonized the Lesser Sunda Isles (proving specifically distinct from *P. nudigula*), Moluccas, and Solomons (proving specifically distinct from *P. implicata*). The resulting widely-separated populations became very different from one another. Internal diversity may have been developed in groups A and B to much the same extent as is seen in group C to-day, before it was obscured by gene-flow. New Caledonia was probably colonized from the Solomons before the development of the special characters of group C, while there was a later expansion to Fiji and on to Samoa. Meanwhile the " *soror* " subspecies had colonized Australia. Because of the more humid climate and frequent emergence of the Arafura shelf during the Pleistocene, its range was probably more or less continuous. Not until the colonization of Southern Melanesia and the separation of northern and southern populations by the Recent eremiation of Australia (Browne, 1945) could the internal differentiation of the *soror* assemblage proceed far.

When the two New Guinea forms invaded one another's ranges as *P. schlegelii* and *P. soror* (their hen-feathered representatives *P. lorentzi* and *P. meyeri* having already done so), a contemporary systematist would have expressed the situation in terms of a superspecies (the *schlegelii* assemblage) overlapping in New Guinea with a polytypic species (the *soror* assemblage). Yet the assemblages fused when they met in the archipelagos, mainly as a result of the explosive expansion of group H (black in right-hand inset, Text-fig. 6). Probably the complex palimpsest produced by new colonists interbreeding with the old, and incorporating characters proper to them, appeared first in New Caledonia at the invasion of Southern Melanesia from Australia.

The origin of group H is obscure. The most distinctive forms belonging to this group are widely separated (p. 160), and so do not help in determining the direction of expansion. Its derivation from one of the groups belonging to the *schlegelii* assemblage would imply too much reversal and convergence to be plausible. Since its common characters are very close to the standard for the whole superspecies, it may even represent a rather conservative though highly adaptable derivative of the common ancestor in New Guinea. Or the resemblance between its Banda Sea and Pacific sections may be convergent. But on the whole group H seems most likely to have arisen from the *soror* assemblage, as a stock adapted to island life, in the Banda Sea. Former island populations between Tenimber H42 and the Louisiades H47 may have become extinct during the Pleistocene fluctuations in sea-level over the Arafura shelf. Whatever its origin, the group has spread widely until its influence is apparent from Java to Tonga, and has interbred with very unlike island forms belonging to both assemblages. At this time the contemporary systematist would have regarded *P. soror* as conspecific with the whole complex of intergrading forms, and would have looked on the superspecies as analogous to a ring species—with *P. soror* and *P. schlegelii* specifically distinct in New Guinea, yet connected through series of interbreeding forms in the archipelagos. The latest major event, the escape of group E from Australia as a colonist of coastal and second-growth formations, shows that this is an oversimplification, and that morphological analogy may be misleading in the assessment of potential isolating mechanisms. Group E penetrated the range of *P. soror* as a distinct, though very similar and closely-related, species ; merged completely with its near relatives of group H in the Louisiades, yet remains more or less isolated from the same group in the Bismarcks ; and has interbred freely with the very dissimilar and phylogenetically distant group C in the Solomons.

Rate of divergence

In general, the degree of difference now to be seen between related forms (both within and between subspecies-groups) agrees reasonably well with the sequence of events suggested above, when the retarding effect of gene-flow between populations has been taken into account. The groups belonging to the *schlegelii* assemblage are much more different from one another than those of the *soror* assemblage. Group C shows the most internal differentiation of any group in the superspecies, while there is considerable variation within group A despite the levelling effect of gene-flow from group H. Group D is evidently derived from group C, and there is remarkably little difference between the populations on Viti Levu and Vanua Levu ; while *P. flavifrons*, derived from group C at second hand, shows no appreciable variation between Savaii and Upolu. The females of group B are so like those of *P. schlegelii* that the populations in the northern Moluccas may have been in genetic contact with those of the Vogelkop long after the invasion of the Lesser Sunda Isles and Solomons, and the slightness of the geographical variation there bears out this supposition.

P. schlegelii and *P. soror* are here supposed to be New Guinea endemics of equal antiquity, and the former to have occupied a discontinuous range before their reciprocal invasions—so that its greater geographical variation is not unexpected. Similarly, the comparative uniformity of the Australian groups agrees with what is known about the rates of divergence in populations of continental and of insular range. In the characters common to most of its members, group G is little more distinct from groups E and F than they are from one another, and combines characters of each (Table IV). This suggests that southern Melanesia may have been colonized at about the time that increasing aridity effectively divided the range of *P. pectoralis* in Australia. However, there is considerable variation within group G (even when the effects of a genetic contribution from the *schlegelii* assemblage to New Caledonia have been allowed for) and the much greater uniformity of groups E and F must be attributed to their more or less continuous continental ranges. Both these groups have isolated representative populations on small islands far from Australia, but hen-feathering on Norfolk Island F33 is the only considerable change shown by these populations. The distribution of group E in New Guinea and the nearby islands strongly suggests the very recent incursion of an ecologically-specialized form, and recent colonization is the probable explanation for lack of divergence on Lord Howe F32 also.

Although there is considerable local variation within group H, widely separated forms are remarkably similar (for example, the females in the southern Moluccas, Bismarcks and Santa Cruz H43–44, 48–49 & 52–53). Apart from the effects of intergradation with other groups, the isolated sections of this group in the Banda Sea, eastern Papuan islands, Santa Cruz and Fijian archipelagos are not well differentiated from one another. It seems probable that most of the large range of this group has been colonized relatively recently, despite the wide scatter of very distinctive forms (p. 160). This conspicuous divergence of some of its members, in one or a few characters, is discussed below (p. 184).

Unexpected uniformity

In some areas there is surprisingly little geographical variation from island to island, although the distances involved are not small in comparison with those between islands occupied by strikingly different forms in other archipelagos. Where there is evidence of gene-flow between groups (as in the Banda Sea, Louisiades and Fiji), it is evident that the populations on different islands are or have been in genetic continuity, and the uniformity may be attributable to swamping. Elsewhere it may reasonably be explained in terms of colonization too recent for much subsequent diversification, as has been suggested for group H as a whole, and for the insular expansions of groups E and F.

But the slightness of the geographical variation within the New Hebrides G36–37f, in contrast to the marked differences between the forms on the different island-groups of Southern Melanesia (G34, 35, 36 + 37, & 38), does not at first sight seem to be susceptible to either of these explanations. There is no evidence for exceptional gene-flow here (except perhaps from New Caledonia G34 to Aneitum G36), and the New Hebridean type is too distinct from its relatives for the whole archipelago to have been colonized only recently. The distances between islands in the New Hebrides are shorter than those separating them from the Loyalty Isles G35 and Vanikoro G38, but there are several gaps (e.g. from Erromango to Efate G37a/b, and from Maewo to Gaua G37e/f) comparable with those which separate very distinct forms on Guadalcanal C11, Malaita C12 and San Cristobal C17, or on New Caledonia G34 and the Loyalty Isles G35. Almost all the New Hebridean gaps are wider than those which separate the three marked races of the central Solomons C13–15.

Much of the New Hebridean avifauna shows this combination of a fairly high degree of endemism with surprisingly slight geographical variation. This might follow if geographical variation were closely related to environmental differences, and if the New Hebrides were environmentally much more uniform than the other archipelagos. But, in *Pachycephala* at least, variation does not seem to be as minutely correlated with demonstrable local differences as this theory would demand, while the New Hebrides show much more variation in climate and vegetation (from a marked dry season, with permanent grasslands, in the south to a very equable equatorial climate, with only rain forest, in the north) than do the Solomons. It seems that for a considerable part of the avifauna, genetic isolation between the islands of the New Hebrides is either imperfect or only recently established. The existing patterns of variation might result from the splitting up of an originally continuous range (by subsidence), or from an expansion into new territory (by island-building or other external changes, since several species are involved).

The geological evidence (Mawson, 1905) is that most of the New Hebridean islands except Malekula and Santo G37d have arisen since the late Pliocene, either by volcanic extrusion or by uplift. The terraced profile of parts of the central New Hebrides is very marked, and quite unlike anything seen in the eastern Solomons (Cain & Galbraith, personal observation). It is possible that geological events, and their ecological consequences, can be invoked in partial explanation of the avifaunal peculiarities of San Cristobal, including the incursion of a Southern Melanesian *Pachycephala* (Galbraith, in preparation).

Unexpected diversity

Some forms, on the other hand, are more different from their close relatives than is to be expected from the suggested sequence of events on the assumption that populations not swamped by gene-flow have diverged at approximately the same rate. The outstanding forms (i.e. A4 & 5; C12, 13, 14, 16 & 17; D21; E27; F33; H42, 52 & 57; *P. flavifrons* (an offshoot of group D), and the subspecies (1) of *P. schlegelii* and *P. soror*) occupy more or less restricted ranges, isolated at the periphery of their respective groups. The law of peripherally-isolated populations (Mayr, 1954b) is well illustrated in areas where geographical variation is less advanced: the comparatively well-marked forms in the northern Moluccas (B7), New Hebrides (G36, & G37a) and Bismarck archipelago (H49–51, & H48d) are all peripheral. Mayr discusses the possible explanations: drift, resulting from small population size; selection, resulting from environmental differences (physical and biotic); and "genetic revolution", resulting from a small gene-pool (initially because of the smallness of the founding population, and subsequently because replenishment by gene-flow is restricted).

Because such aberrant peripherally-isolated populations often occupy relatively small islands, drift has been invoked to explain them. But few forms of *P. pectoralis* are found on tiny islets (the exception, group E, has as yet diverged little over a widely scattered range), and it is improbable that the local effective breeding populations of this common bird are sufficiently small for selection to be overcome by random fixation and elimination of genes.

The brownness of the females of both *P. schlegelii* and *P. soror* in the Vogelkop may be an adaptation to very humid conditions (p. 177), while there is evidence of the selective influence of climate on *P. pectoralis*, not only in Australia but to some extent in the archipelagos (p. 187). Certain regularities of geographical variation in different bird species suggest that the physical environment varies from island to island more than is generally supposed, and considerable local differences in climate between habitats within one island support this view (Cain, unpublished). Unfortunately, meteorological data for this region are scanty, and are probably affected less by the relatively slight changes in average climate from island to island than by the precise siting of the stations. Although differences in the physical environment cannot be ruled out, the diversity of characters involved makes it necessary to look further for the causes of differentiation in peripherally-isolated forms.

Biotic differences (especially in the avifauna) seem more promising, but are still more difficult to assess. Trends in the dimensions of forms on small islands are discussed below (p. 188), and are probably related to ecological redeployment. Most of the divergent forms occur in avifaunas which are relatively poor in species, and most of the variations in male plumage reduce the distinctiveness of the pattern. But the two features of the avifauna which are most likely to impinge on the visual properties of the pattern—the presence or absence of visual predators, and of species with similar patterns—do not provide a comprehensive explanation of the variation. Lack of visual predation might be expected to relax dorsal crypsis, and in fact two of the the three forms with black mantles are restricted to islands without known hawks (Samoa (*P. flavifrons*), and Ndeni and Santa Cruz islets H52). But both *Accipiter novaehollandiae* and *A. albogularis* are found on Vella Lavella together with the black-mantled *Pachycephala* C13, and the latter hawk may have been overlooked on Ndeni. Only in Australia and New Guinea, the Lesser Sunda Isles and New Caledonia does *P. pectoralis* overlap with other *Pachycephala* species having similar male patterns (*P. soror, P. schlegelii, P. aurea, P. rufiventris* and *P. lanioides*). The loss of the gorget on Malaita C12, for example, is not solely related to the absence of such species, since the only other *Pachycephala* in the Solomons (*P. implicata*) is restricted to the mountains of Bougainville and Guadalcanal and does not have a conspicuous pattern. But such a loss might be disadvantageous in a richer avifauna containing species of similar plumage and behaviour patterns.

Mayr (1954*b*) has pointed out that when an island is colonized by a few stray pairs from a large and genetically variable population, the initial representation of genes will be more or less random . The selective changes involved in regaining a coadapted genetic system will depend on the genes available, so that unpredictable differences between isolated populations arising in this way are to be expected. However, in all these populations there will be selection in favour of genes which have a favourable effect in the homozygote and are at an advantage against a more uniform genetic background, so that some regular trends may be looked for. Both these expectations are fulfilled in *P. pectoralis*. Most of the variations seem to appear entirely at random, yet the ones which strikingly affect the pattern occur only in such peripheral localities. Melanism of the mantle is confined to more or less isolated forms on rather small islands (Djampea, Kalao tua and Madu, Vella Lavella, Ganonga, Rendova and Tetipari, Ndeni and the Santa Cruz islets, Taviuni, Koro, Ngau, Ongea Levu, Fulanga and Wangava, and Upolu and Savaii). Furthermore, the traces of gene-exchange between populations separated by several miles of sea are unusually clear in *P. pectoralis*, and the rapid falling-off in gene-flow with increasing distance will obviously have important genetic effects in this species.

ADAPTATION

Character and climate

The adaptive significance of geographical variation in relation to climatic differences emerges most clearly in continental areas, exposed to regular climatic gradients and occupied by continuous populations. Irregular differences in climate, and the effects of isolation and bursts of colonization by different stocks, make it difficult to correlate character and climate in insular regions (cf. Snow, 1954). In many species of birds, clinal changes are strongly marked from north to south down the eastern coast of Australia, in relation to decreasing average temperature. In this area *P. pectoralis* presents the appearance of a series of isolates with secondary intergradation, rather than of a continuous cline (Mayr, 1954*a*). The Tasmanian population F29 is isolated by sea, and there seems to be a gap in the range of the species between southern Queensland F31a and the rain-forests around Cairns F31b. There is no reason to doubt that the populations from eastern Victoria to southern Queensland F30a–31a are continuous, and material from intermediate localities may show the phenotypic changes to be gradual.

We may arrange the three presumptive isolates of the east coast in a southwards series ; and since groups E and F are closely related we may perhaps add the Northern Territory isolate as a first member. If the northern Queensland populations F31b were included, they would introduce a slight reversal of the otherwise progressive changes. There has evidently been gene-flow from this region into Cape York and across the Torres Straits, and it seems possible that reciprocal flow has produced a retardation of the female characters here (p. 166). Therefore the southern Queensland form F31a instead will be taken to represent group F in the north of its range. Our series from north to south is then : (a) Northern Territory E23, (b) southern Queensland F31a, (c) eastern Victoria F30a, (d) Tasmania F29. In this series the following progressive (though neither smooth nor synchronous) changes are apparent :

(i) increasing wing-length (and presumably body-size) ;
(ii) increasing relative tail-length ;
(iii) decreasing absolute and relative bill-size ;
(iv) decreasing amount of solid black (in the male tail) ;
(v) decreasing concentration of carotenoid (female plumage and male tail especially).

Such a series of progressive changes might be maintained without climatic adaptation, by gene-flow from end-forms which had diverged in isolation. The characters of an intermediate population would then depend mainly on its degree of genetic isolation from each gene-source. However, changes (i), (iii) and (iv) (increasing body size, decreasing relative length of appendages and concentration of melanins) are sufficiently general among homoiothermous animals, in relation to increasing latitude, to be recognized as Bergmann's, Allen's and Gloger's ecological rules (see Huxley, 1942). Furthermore, all five of these changes are paralleled in Palaearctic titmice (*Parus* spp., Snow, 1954), in relation to decreasing temperature. It is most probable that the changes seen in *P. pectoralis* in eastern Australia are likewise adaptive. In certain other parts of the species-range parallel trends are discernible, although (as in *Parus*) there are numerous exceptions among island forms.

From the Northern Territory to midwestern Australia (E23–22a), solid black and intensity of diffuse melanin and of carotenoid decrease, but wing-length also decreases and proportions are not much affected. The small size and general pallor of these forms are paralleled in group A of the Lesser Sunda Isles, and it is noteworthy that these two areas are the driest occupied by the superspecies. In many groups of birds (Snow, 1954 ; Cain, unpublished), intensity of pigmentation falls off with decrease both in temperature and in humidity. This applies both to melanins (Gloger's rule) and to carotenoids. In arid regions the range of temperature is great, and it may be that coloration and body-size are responding to lower minimum and higher maximum temperatures respectively.

In group G, the male tail is black in the north G38, olive in the south G34–36, and olive with black subterminally in the centre of the range G37. There is a southwards decrease in the intensity of carotenoid, especially in the females, from Vanikoro G38 through the New Hebrides as a whole G36–37 (with local variation) to New Caledonia G34 ; but the Loyalty Isles race G35 is yellowest of all, and no corresponding regularities in the variation of size and proportions are apparent. Throughout the archipelagos there are such hints of climatic correlations, but the exceptions are so numerous that they cannot be relied upon. Thus at the level of the subspecies-groups within the *schlegelii* assemblage, it might be suggested that the low intensity of carotenoid in the females of groups A and D is correlated with the aridity of the Lesser Sunda Isles and the coolness of Fiji respectively ; while in the hot and moist Moluccas females of group B have intense yellow pigment. But there is as great variation in this character between adjacent islands of the Solomons (C9, 11 & 12 against 10 & 13–17), whose climates cannot be very different. Another possible climatic correlation, since both localities are rather arid, is in the appearance of a pinkish phaeomelanic wash over breast and belly of the females in southern Australia F28 and on Timor H39. But the appearance of the character also on small islands of the Flores Sea A4, and its absence from females of group E from the most arid parts of Australia, seem to contradict this. As in Palaearctic tits, climatic correlations are merely hinted at among isolated forms.

Character and habitat

In New Guinea members of the superspecies occupy different altitudinal belts, with more or less overlap, from coastal second-growth (*P. pectoralis* E24) through hill forest (*P. soror*) and lower montane cleared land (*P. pectoralis* E27) to mountain forest (*P. schlegelii*). The three highland forms of this series agree in the olivaceous wash on the underparts of their females—found elsewhere in the superspecies only in forms derived from *P. schlegelii*. The relict species *P. nudigula* and *P. implicata* (in the mountains of the Lesser Sunda Isles and Solomons) also show this character, which thus seems to have been independently acquired about five times by members and close relatives of the *pectoralis* superspecies, in relation to life at higher altitudes. The males also of *P. nudigula* and *P. implicata* are strongly washed with olive beneath, while those of *P. soror* have an olivaceous appearance (due largely to the long grey feather bases showing through). Possibly the rufous ventral wash of male *P. schlegelii* represents a parallel adaptation to high altitudes. The small size of the white throat-patch in *P. schlegelii* and *P. soror*, the reappearance of grey bases to the white feathers in *P. pectoralis* E27, and the greying or blackening of the throat in *P. nudigula* and *P. implicata* may also be parallel responses to similar environments. All these trends are towards the blurring of the conspicuous ventral pattern (obscured also in the montane species *P. rufinucha*, *P. tenebrosa* and *P. olivacea*).

Several subspecies have been described from the Banda Sea, which inhabit small islands and closely resemble those of adjacent large islands, but which are described as being larger, with conspicuously larger bills and often with more golden-olive mantles. This is true of Lomblen, Pantar and Alor A3b compared with Sumbawa and Flores A3a; Wetar H39b compared with Timor H39a; Amboina H43b compared with Ceram H43a; and Ternate and Tidore B7 compared with Morotai, Halmahera and Batjan B6. Unfortunately the series of several of these forms available to the authors of the descriptions and to me are not adequate for the statistical significance of the differences to be determined. In the Bismarck archipelago the populations on Lihir and Tabar H49–50 are conspicuously larger and larger-billed than those of the large islands H48 & 51. The same is true of *dahli* E25 in comparison with its close relatives in northern Australia E23 (the populations E25 lying between, being affected by gene-flow, are ineligible for comparison) and of the races on Lord Howe and Norfolk Islands F32–33 in comparison with the parental populations at the same latitudes in Australia F31a. All the races which are strikingly larger than their close relatives (and have correspondingly large bills) occupy small or low-lying islands: Ternate and Tidore B7, the Loyalty Isles G35, the Tenimber Isles H42, Lihir and Tabar H49 & 50, and Tonga H57. This tendency towards large size, and particularly towards large bill size, is well known among insular birds

(Murphy 1938 ; Mayr & Vaurie 1948), and may be related to redeployment of the few species on such islands among the available food niches. However, Mayr's figures (1932*a*, *b*) do not suggest any such general rule in the Solomons, Santa Cruz, New Hebrides and Fiji, for situations where closely related populations occupy neighbouring islands of different sizes.

It has already been noted that markedly divergent subspecies occur on rather isolated, and usually small, islands. Apart from the effects of isolation and the small gene-pools of founding populations, the relative paucity of species on these islands may have been an important factor in permitting the male pattern to diverge widely from the standard. For example, in group A hen-feathering occurs on Salayer A5 (about 35 resident land bird species) and melanism of the mantle on islands in the Flores Sea (about 55 species), whereas the male on Sumba A1 (about 110 species) is ventrally conspicuous and dorsally cryptic. In group C hen-feathering occurs on Rennell C16 (about 35 species) and melanism on peripheral islands of the central Solomons C13–14 (about 60 species), while the male on Guadalcanal C11 (about 95 species) is standard for the group. The male on Norfolk Island F33 (about 15 species) is hen-feathered, unlike its relatives in eastern Australia F30–31 (several hundred species). The mantle is wholly black on Ndeni and the Santa Cruz islets H52 (about 20 and 10 species respectively), and in *P. flavifrons* of Samoa (about 30 species). In Fiji the correlation with avifaunal poverty is less clear : black-mottled mantles occur on Koro, Ngau and the southern Lau archipelago D20b, H55-56 (25–30 species) and not on Viti Levu (about 50 species) ; but on two islands with apparently similar avifaunas (about 40 species), black mottling appears on Taviuni D20a but not on Vanua Levu D19a. It may be that further species remain to be discovered on Vanua Levu, a large and mountainous island, whereas Taviuni is smaller and better known. But elsewhere, too, the realization of these trends seems capricious. Although neither hen-feathering nor melanism of the mantle occur where the avifauna is rich, they are not always present where it is poor. Well-marked races which do not show these tendencies occur on the following small, low or isolated islands : Tidore and Ternate B7, Russel Islands C10c, Vatu vara D21, Lord Howe F32, Loyalty Islands G35, Aneitum G36, Vanikoro G38, Wetar, Babar, Damar and Tenimber H39b–42, Lihir, Tabar and Manus H49–51, Utupua H53, Kandavu H54 and Tonga H57.

Variation in habitat

The members of the *pectoralis* superspecies throughout its range are forest birds which forage for soft-bodied insects (and some berries) among the twigs and branches of the substage and lower canopy. Field notes are rare in the literature, but it is clear that there is considerable variation in the habitats selected by different forms. The altitudinal deployment in New Guinea has already been mentioned, and races of *P. pectoralis* are found at different altitudes on different islands.

Group A is found only above 6,500 ft. in eastern Java A2a and above 3,000 ft. on Bali A2b, but from 4,000 ft. down to sea-level on Flores A3a (Hartert, 1897 ; Stresemann, 1913 ; Meise, 1929 ; Rensch, 1931 ; Hoogerwerf, 1948). This may be related to the presence of the lowland *P. grisola* on Java and Bali, and of the mountain *P. nudigula* on Flores.

Altitudinal preferences are known to differ from island to island in the Solomons, though the details remain to be worked out. Mayr (1932*a*) reports the species as rare or absent in the lowlands of Bougainville and Malaita C9 & 12, though common near the coast on Choiseul C10a. Cain and Galbraith (1956) heard it occasionally in the lowland forest on Guadalcanal C11, but found it much more common in the hill forest at about 2,000 ft., and up to the lower limit of the mist forest (where it is replaced by *P. implicata*). On San Cristobal C17 I found it to be common at 2,000 ft. and down to the coast. It is recorded by Donaghho (1950) in the lowland forest on Guadalcanal, but not by Sibley (1951) in the same habitat on New Georgia C15.

The altitudinal preferences of *P. pectoralis* in the northern Moluccas and Fiji do not seem to have been recorded. *P. flavifrons* is found at 600 ft. and above on Upolu (Nicoll, 1904).

On Timor H39a, *P. pectoralis* occupies a greater vertical range than has been recorded elsewhere, from sea level to 7,500 ft. (Stein, 1936; Mayr, 1944*c*). It is absent from the lowlands (occupied by *P. rufiventris*) on Ceram H43a and Buru H44, and reaches 5,000 ft. (Stresemann, 1914*a*, *b*). Scott (1946) records it on Santo G37d as commonest in the higher forest, though frequent also in the open lowland forest. I have seen it on that island and on Efate G37b in tangled second growth near the shore, a habitat never seen to be occupied by the species on Guadalcanal and San Cristobal. In southern and eastern Australia it is found in dense and open forest (records in the *Emu*, 1902 to date), but not in the dense myrtle-beech forest of the wettest areas on Tasmania F29 (Lawrence, 1952), where *P. olivacea* is found.

The most striking specialization in habitat is found in group E. This occupies mangroves fringing the deserts of north-western Australia E22; mangroves, coastal forest and second growth from northern Australia to the Bismarcks and Solomons E23–26 (especially on very small islands); and second growth in the highlands of New Guinea E27. This specialization has allowed it to penetrate the ranges of the deep-forest forms *P. schlegelii*, *P. soror* and *P. pectoralis* H48. Although the two males E25 and H48 in the Bismarcks are similar in appearance, they differ markedly in habitat, conspicuousness and song (Dahl, 1899). As a consequence of their different habitat-preferences, members of group E must be exposed to different micro-climates from the neighbouring forest races. The special conditions in desert-fringing mangroves (presumably humid, yet subject to extremes of temperature) may explain the apparently contradictory changes of phenotype in north-western Australia E22 (p. 187).

The variability of the hybrid populations on small islands off Shortland E26 may well be maintained by selection in relation to habitat differences. These populations are separated from one parental stock (C9) by less than three miles, from the other (*dahli* E25k) by almost two hundred. The latter occupies islets such as these, which elsewhere in the Solomons have no *Pachycephala*. Presumably the hybrids are better adapted to small islands than are the pure forms of group C. A surprising feature of the hybrid sample is that the smallest males have the whitest throats (like the small *dahli*) and the largest the yellowest throats (like the large Shortland race). In isolation, genetic linkage alone could keep the recombination classes scarce in the population for a few generations only. This would imply that at the time the known specimens were collected (1927) the hybrid populations were very young indeed, in which case they may by now have become partly stabilized. Supposing the situation to be of longer standing than this implies, the observed co-variation might be achieved by continued gene-flow from the parental stocks, or by selection in favour of the parental genotypes, or both. Recolonization by *dahli* must be almost unknown, while birds may arrive from Shortland rather frequently. In view of the failure of group C to colonize habitats such as are occupied by the hybrids, it seems probable that the *dahli* genotype is being maintained by selection, in the face of gene-flow from Shortland.

Variation in bill size

The absolute and relative length and stoutness of the bill varies greatly within the superspecies, to an extent which in many groups of birds would be considered to warrant generic separation. But the colour-patterns of the males are so clearly allied to one another that even Mathews (1930) places all these forms in a single genus. The variation shown by the bill is largely independent of the major discontinuities, and certain regularities apparent in a cursory study (pp. 186 and 188) show it to be at least partly adaptive. It is therefore relatively unimportant in the study of relationships within the group, and has not been dealt with in this paper.

Except in long series, the finer geographical variation is to some extent obscured by individual variation and the inaccuracies of measurement (especially of bill depth). The tables (p. 217) give some idea of the range in length and stoutness. Evidently very different bills (e.g. massive in Tenimber H42, slender in the Louisiades H47 and stubby in Tasmania F29) must be best adapted to taking correspondingly different food. But almost nothing is known about geographical differences in diet. The Guadalcanal race C11 takes considerably larger insects on the average than the smaller race, with a shorter and finer bill, on San Cristobal C17 (Cain & Galbraith, 1956). Dahl (1899) records that of the two stocks in the Bismarcks, *dahli* E25 (with slightly the longer bill) takes a proportion of vegetable matter, while the race on the large islands H48 does not.

CONCLUSIONS

The very different plumage patterns of the sexes provide a large number of more or less independent characters which vary in stability and systematic importance, from the " qualitative " characters which unite males of the *schlegelii* assemblage to the slight differences in pigmentation and dimensions which distinguish closely-related populations on neighbouring islands. This makes it possible to study relationships within the superspecies despite the independent origin and loss of even the most stable characters, since the local co-variation of several relatively labile characters can be of equal importance. Most of the stable characters are provided by the male pattern, and most of the more plastic ones by that of the female. The relationships suggested in this paper could not all have been arrived at by considering one sex alone, and it may not be possible to decide with any certainty the affinities of hen-feathered species such as *P. simplex*, *P. sulfuriventer* and *P. philippensis*. In organisms which do not show such diversity in conventional museum material, a genetic situation of equal complexity could only be interpreted by bringing in further characters (whether of internal anatomy, cytology, genetics, biochemistry, physiology, ecology or behaviour), which are most desirable in this group also, to test the validity of conclusions based entirely on a study of skins (cf. Wilson & Brown, 1953).

The combination of great colonizing ability (implying dispersal) and divergence of neighbouring populations (implying philopatry) shown by the *P. pectoralis* superspecies is remarkable, though not unprecedented. However, *P. pectoralis* is unique in having so many and so diverse forms, all of which are strictly allopatric, and between the most dissimilar of which there has been extensive gene-exchange. In this superspecies hybridization and sympatry are largely independent of phylogenetic relationships, cutting across the division into *schlegelii* and *soror* assemblages. It seems to be impossible to predict whether or not any given pair of representatives would interbreed on coming together, by considering only their resemblance and relationship. Purely local adaptations to the environment, and the manner of their meeting, are perhaps important in determining the outcome (p. 179). Although at the species level we have an objective criterion, not found higher or lower in the systematic hierarchy, for the relative status of any two populations which come in contact, it may not always be possible to use this criterion quite consistently in delimiting a given species. Strictly there are no biospecies, but only biospecific relations between sympatric populations. In the *P. pectoralis* superspecies, however, the three species *P. schlegelii*, *P. soror* and *P. pectoralis* can be satisfactorily delimited—although the different relationships between groups E and H in the Louisiades and Bismarcks (p. 168) suggest that in other groups it may be necessary to draw species-limits more arbitrarily. Morphological analogy is still the only available yardstick in determining the status of isolated representatives ; but the co-existence of closely-related forms in New Guinea, and interbreeding between more distant relatives in the archipelagos, demonstrate that other factors must be taken into account. Though at present we can only speculate on the nature of these factors, we need not consider as distinct species all those geographical representatives which are more different than the most similar pair of related sympatric species. It is justifiable and expedient to admit a wider range of representative forms to a single species than is the current practice. (In accordance with this consideration the Guadalcanal representative of *Cichlornis whitneyi* Mayr has been described as a subspecies (Cain & Galbraith, 1955), although the differences between it and the form in the New Hebrides are greater than those between many sympatric pairs of warblers.)

The pattern of variation shown by the superspecies is interpreted as the result of colonizations by two stocks which diverged in New Guinea and attained biospecific relations with one another there, yet interbred freely in the surrounding archipelagos. The Lesser Sunda Isles, Moluccas and Solomons seem to have been colonized independently at an early date, from western and northern New Guinea, while the peculiar forms in northern Fiji and Samoa represent colonists from the Solomons (from which the New Caledonian race may also have received a contribution). Southern Melanesia is populated by forms which must have come from Australia at a later date (and which probably in turn colonized San Cristobal). Gaps in the range of these groups, from the Banda Sea through the western Papuan islands and Santa Cruz to southern Fiji and Tonga, are occupied by a relatively undifferentiated stock which must have expanded relatively recently, and has formed hybrid populations with all the older groups with which it has come in contact. Finally, the stock which in northern Australia had become ecologically specialized for life in coastal and second-growth formations, has thereby been enabled to penetrate similar habitats in New Guinea and the eastern Papuan islands—sometimes merging completely with resident forms, sometimes remaining more or less isolated from them.

This distributional history accords well with the avifaunal peculiarities of the sub-regions within Australasia, exemplifying several trends. For example, *P. pectoralis* is essentially an Australasian bird—but it slightly transgresses Wallace's Line and is stopped, not by the edge of the Sunda shelf, but presumably by the moister conditions and richer avifauna of western Java. Mayr (1944*a*) has shown that for the avifauna as a whole the Lombok Strait is merely the most effective single barrier in the series presented by water gaps and climatic differences along the Sunda Isles route. As is true of many birds, the species is represented by a peculiar form on the Tenimber Isles. The invasion from the Cape York peninsula of the relatively dry areas of southern and south-eastern New Guinea is paralleled by several species (e.g. *Pachycephala rufiventris*, *Myiagra rubecula*; and see distribution maps in Mayr, 1944*b*).

In the south-west Pacific the history of the species is representative for important elements of the avifauna. The Solomons are occupied by an ancient and peculiar endemic group, derived from New Guinea and showing extreme variation from island to island, whereas the Bismarcks have evidently been colonized only comparatively recently. A stock from Australia has occupied southern Melanesia and continued to San Cristobal (where the endemic form exemplifies several trends), and the New Hebrides are occupied by rather uniform populations. Both the northern Moluccas and the Solomons have well marked forms, belonging to the *schlegelii* assemblage and contrasting with those of the Banda Sea and eastern Papuan islands; but these are independently derived from *P. schlegelii* rather than directly related to one another. Faunal affinities between the two regions have been pointed out (Zeuner, 1943, 173 for *Troides* and Hale Carpenter, 1953, 149 for *Euploea* (Lepidoptera); Voous & van Marle, 1949, for *Coracina*), and others might be suggested (e.g. *Eos, sensu stricto*, and "*Eos*" *cardinalis*; *Dicaeum erythrothorax* and *D. aeneum*; *Rhipidura rufiventris cinerea-obiensis* and *Rh. cockerelli*). The authors quoted postulate a continuous island chain, broken by the northwards drift of New Guinea as recently as the Pliocene; but the explanation put forward for *Pachycephala* may be more acceptable—common origins in New Guinea, with parallel evolution under the effects of similar climates, avifaunas and degrees of isolation.

No mention has been made of primitive characters. These can, of course, be recognized only from their occurrence and co-variation, not on *a priori* grounds. Clearly the immediate common ancestor of the superspecies was not hen-feathered but sexually dimorphic, and sexual dimorphism has been lost independently three times in *P. pectoralis* (and in the opposite way by *P. flavifrons*). Other striking characters are similarly debarred from consideration by their scattered or peripheral distribution.

It is reasonable to suppose that the proto-*schlegelii* showed the black chin and overlapping throat-feathers which characterize members of the assemblage derived from it. But, without making unjustifiable assumptions about the possibility of independent origin or secondary loss of characters, it does not seem that anything can usefully be said about the other characters of this form, or about the common ancestor of both assemblages. Since the striking male variants from the standard pattern mostly reduce its distinctiveness, and since degenerative changes under relaxed selection probably proceed more quickly than selective enhancement of the pattern's visual properties, it is rather more likely that in any given instance the direction of evolution was away from the standard. But not even as much as this can be said of the labile female pattern.

SUMMARY

1. *Pachycephala pectoralis*, *P. soror*, *P. schlegelii* and *P. flavifrons* are considered to belong to a single superspecies, represented by a doublet in New Guinea (*P. soror* and *P. schlegelii*) with which *P. pectoralis* overlaps slightly. Standard patterns for males and females are pragmatically defined, and character-geographies of a number of the more clearly-defined variants given. Despite the independent origin and loss of characters, natural groups of subspecies can be distinguished (though not diagnosed) by considering the whole constellation of characters, weighted according to their co-variation. However, extensive secondary intergradation makes some of the boundaries between groups vague.

2. A great range of forms is connected by intergradation, and must be considered as a single species (*P. pectoralis*), although in New Guinea a pair of close relatives co-exist. It is concluded that conspecific allopatric forms may be more different than sympatric species, and *P. caledonica* of New Caledonia and *P. melanops* of Tonga are accordingly admitted to *P. pectoralis* (as is *P.* " *orpheus* " *teysmanni* of Salayer). The ability to interbreed is shown to be largely independent of relationship, and the species-limits to cut across the phylogenetic classification.

3. Current criteria for the recognition of subspecies are criticized, and a higher standard of difference applied, in a subspecies-arrangement of *P. pectoralis* designed to reveal more clearly the uniformities and discontinuities. It is not suggested, however, that this arrangement should be adopted at present, and a list of subspecies to be recognized according to current practice is provided in the appendix.

4. The distributional history of the superspecies is considered, and it is concluded that *P. soror* and *P. schlegelii* are descended from former geographical representatives within New Guinea. Near-standard subspecies of *P. pectoralis* in Australia, Southern Melanesia and elsewhere are closely related to *P. soror*, yet intergrade extensively with the peculiar endemic forms of the Lesser Sunda Isles, Moluccas, Solomons and Fiji—whose affinities are rather with *P. schlegelii*. But this view does not necessarily imply reticulate evolution, in the sense of a breakdown of established interspecific barriers.

5. As might be expected from theoretical considerations and studies on geographical variation in other animals, few correlations with climate or habitat can be detected within the insular range of *P. pectoralis*. In Australia, however, regularities are

apparent which agree with the well-established ecological rules of variation in homoiothermous animals ; and certain trends are apparent in forms which inhabit high altitudes, small islands, and islands where there are few bird species. There are in addition progressive character-changes in several insular areas, but most of these are interpreted as the result of secondary intergradation between forms of different origin. The geographical pattern of variation in these areas is consistent with the hypothesis of gene-flow, with peripherally-isolated forms shielded from its effects. It is possible that certain characters tend to appear especially in forms of hybrid origin.

CHECKLIST

Synonyms given by Mathews (1930) and Mayr (1932*a*, *b*, 1941*a* and 1954*a*) are not quoted here. A list of the subspecies to be recognized according to current practice is given on p. 205.

PACHYCEPHALA SCHLEGELII Schlegel

1 ***Pachycephala schlegelii schlegelii*** Schlegel.

Pachycephala Schlegelii Schlegel, 1871 (from MS von Rosenberg). Tijdschr. ned. dierk. Ver. **4**, p. 43—l'intérièur de la Nouvelle-Guinée [Arfak Mountains, according to Mayr, 1941*a*, 149].

Range : mountains of the Vogelkop, and Wandammen Mountains.

2 ***Pachycephala schlegelii cyclopum*** Hartert

Pachycephala schlegelii cyclopum Hartert, 1930. Novit. zool. **36**, p. 54—Cyclops Mountains.

Range : Cyclops Mountains.

3 ***Pachycephala schlegelii obscurior*** Hartert

Pachycephala schlegelii obscurior Hartert, 1896. Novit zool. **3**, p. 5—Eafa District [Owen Stanley Mts.].

Pachycephala schlegelii viridipectus Hartert & Paludan, 1936. Mitt. zool. Mus. Berlin, **21**, p. 203—Kunupi [Weyland Mts.].

Range : (a) Weyland, Nassau and Oranje Mountains (" Snow Mountains ") intergrading with (b) Saruwaged and Sepik Mountains, and mountains of south-eastern New Guinea.

PACHYCEPHALA SOROR Sclater

1 ***Pachycephala soror soror*** Sclater

Pachycephala soror Sclater, 1873. Proc. zool. Soc. Lond. p. 692—Atam [Hatam], Arfak Mountains.

Range : mountains of the Vogelkop.

2 ***Pachycephala soror klossi*** Ogilvie-Grant

Pachycephala soror klossi Ogilvie-Grant, 1915. Ibis Jubilee Suppl. No. 2, p. 88—the Utakwa Valley.

Range: (a) mountains of northern New Guinea (Mamberano) and Weyland, Nassau and Oranje Mountains ("Snow Mountains"), intergrading with (b) Hagen, Bismarck and Saruwaged Mountains.

3 ***Pachycephala soror bartoni*** Ogilvie-Grant

Pachycephala soror bartoni Ogilvie-Grant, 1915. Ibis Jubilee Suppl. No. 2, p. 89—British New Guinea [Type: Owen Stanley Range, 5,000 ft.].

Range: mountains of south-eastern New Guinea and Goodenough Island.

PACHYCEPHALA PECTORALIS (Latham)

A1 ***Pachycephala pectoralis fulviventris*** Hartert

Pachycephala fulviventris Hartert, 1896. Bull Brit. orn. Cl. **5**, p. 47—Sumba.

Range: Sumba.

A2 ***Pachycephala pectoralis javana*** Hartert

Pachycephala pectoralis javana Hartert, 1928. Bull. Brit. orn. Cl. **48**, p. 88—Mt. Ardjuino, East Java.

Range: (a) eastern Java, intergrading via (b) Bali with A3.

A3 ***Pachycephala pectoralis fulvotincta*** Wallace

Pachycephala fulvotincta Wallace, 1863. Proc. zool. Soc. Lond. p. 492—Flores.
Pachycephala pectoralis jubilarii Rensch, 1929. J. Orn. Lpz. Festschr. p. 202—Alor.

Range: (a) Sumbawa and Flores, (b) Lomblen, Pantar and Alor.

A4 ***Pachycephala pectoralis everetti*** Hartert

Pachycephala everetti Hartert, 1896. Novit. zool. **3**, p. 170—Insula Djampea.
Pachycephala pectoralis atromaculata Meise, 1929. J. Orn. Lpz. **77**, p. 448—Kalao tua.

Range: Djampea, Kalao tua and Madu.

A5 ***Pachycephala pectoralis teysmanni*** Büttikofer

Pachycephala teysmanni Büttikofer, 1893. Notes Leyden Mus. **15**, p. 167—Macassar, South Celebes [corrected to Salayer by Meyer & Wigglesworth, 1898, Birds of Celebes, **2**, p. 397].

Range: Salayer.

B6 ***Pachycephala pectoralis mentalis*** Wallace

Pachycephala mentalis Wallace, 1863. Proc. zool. Soc. Lond. p. 30—Batjan et Gilolo [Type: Batchian].

Pachycephala pectoralis gilolonis Kuroda, 1938. Tori. **10**, p. 114—Halmahera.

Range: Morotai, Halmahera and Batjan.

B7 ***Pachycephala pectoralis tidorensis*** van Bemmel

Pachycephala pectoralis tidorensis van Bemmel, 1939. Treubia, **17**, p. 99—Tidore.

Range: Tidore and Ternate.

B8 ***Pachycephala pectoralis obiensis*** Salvadori

Pachycephala obiensis Salvadori, 1878. Ann. Mus. Stor. nat. Genova, **12**, p. 330—in Obi.

Range: Obi Islands.

C9 ***Pachycephala pectoralis bougainvillei*** Mayr

Pachycephala pectoralis bougainvillei Mayr, 1932. Amer. Mus. Novit. No. 522, p. 10—Bougainville Island, Solomon Islands.

Range: Buka, Bougainville and Shortland.

C10 ***Pachycephala pectoralis orioloides*** Pucheran

Pachycephala orioloides Pucheran, 1853. Voy Pôle Sud. Zool. **3**, p. 57—îles Salomon (San-Jorge).

Pachycephala pectoralis pavuvu Mayr, 1932. Amer. Mus. Novit. No. 522, p. 15—Banika Island, Pavuvu or Russel group, British Solomon Islands.

Range: (a) Choiseul, (b) Ysabel, St. George and Florida Islands, (c) Russel Islands.

C11 ***Pachycephala pectoralis cinnamomea*** (Ramsay)

P.[seudorectes] cinnamomeum Ramsay, 1879. Nature, Lond., **20**, p. 125—Guadalcana.

Range: Guadalcanal.

C12 ***Pachycephala pectoralis sanfordi*** Mayr

Pachycephala sanfordi Mayr, 1931. Amer. Mus. Novit. No. 504, p. 22—Malaita Island, British Solomon Islands.

Range: Malaita.

C13 ***Pachycephala pectoralis melanonota*** Hartert

Pachycephala melanonota Hartert, 1908. Bull. Brit. orn. Cl. **21**, p. 106—Vella Lavella I., Central Group of the Solomon Islands.

Range: (a) Vella Lavella, (b) Ganonga.

C14 ***Pachycephala pectoralis melanoptera*** Mayr

Pachycephala pectoralis melanoptera Mayr, 1932. Amer. Mus. Novit. No. 522, p. 18—Tetipari, central Solomon Islands.

Range: Rendova and Tetipari.

C15 ***Pachycephala pectoralis centralis*** Mayr

Pachycephala pectoralis centralis Mayr, 1932. Amer. Mus. Novit. No. 522, p. 15—Vangunu Island, central Solomon Islands.

Range: Kulambangra, New Georgia, Vangunu and Gatukai.

C16 ***Pachycephala pectoralis feminina*** Mayr

Pachycephala feminina Mayr, 1931. Amer. Mus. Novit. No. 486, p. 25—Rennell Island.

Range: Rennell.

C17 ***Pachycephala pectoralis christophori*** Tristram

Pachycephalus christophori Tristram, 1879. Ibis, 4th ser., **3**, p. 441—Makira Harbour, San Cristoval, Solomon Islands.

Range: (a) San Cristobal, (b) Santa Anna.

D18 ***Pachycephala pectoralis graeffii*** Hartlaub

Pachycephala græffii Hartlaub, 1866. Ibis, new ser., **2**, p. 172—Viti-levu.
Pachycephala (?) *optata* Hartlaub, 1866. Ibis, new ser., **2**, p. 172—Ovalau.

Range: (a) Viti Levu and Waia, intergrading through (b) Ovalau with D20b.

D19 ***Pachycephala pectoralis aurantiiventris*** Seebohm

Pachycephala aurantiiventris Seebohm, 1891. Ibis, 6th ser., **3**, p. 96—Bua in Vanua Levu.

Pachycephala pectoralis ambigua Mayr, 1932. Amer. Mus. Novit. No. 531, p. 16—Rambi Island, Fiji Islands.

Range: (a) Yanganga and most of Vanua Levu, intergrading via (b) Thaukandrove Peninsula and (c) Kio and Rambi with D20a.

D20 ***Pachycephala pectoralis torquata*** Layard

Pachycephala torquata Layard, 1875. Proc. zool. Soc. Lond. p. 150—Taviuni.

Pachycephala pectoralis koroana Mayr, 1932. Amer. Mus. Novit. No. 531, p. 15—Koro Island, Fiji Islands.

Range: (a) Taviuni (intermediate between D19c and D20b) and (b) Koro.

D21 ***Pachycephala pectoralis bella*** Mayr

Pachycephala pectoralis bella Mayr, 1932. Amer. Mus. Novit. No. 531, p. 14—Vatu vara Island.

Range: Vatu vara.

E22 ***Pachycephala pectoralis melanura*** Gould

Pachycephala melanura Gould, 1842. Proc. zool. Soc. Lond., p. 134—North coast of Australia [Derby, according to Mathews 1920, p. 229].

Eopsaltria hilli Campbell, 1910. Emu, **10**, p. 168—Hecla Island, Parry Harbour, North-West Australia.

Pachycephala melanura bynoei Mathews, 1918. Aust. avian Rec. **3**, p. 136—Port Hedland.

Range: (a) North West Cape to De Grey River, (b) Broome, (c) King Sound, (d) Hecla Island (off Cape Bougainville) and Napier Broome Bay—clinal series, confined to mangroves.

E23 ***Pachycephala pectoralis violetae*** Mathews

Pachycephala gutturalis violetae Mathews, 1912. Aust. avian Rec. **1**, p. 76—West Northern Territory [Daly R., according to Mathews 1920, p. 224].

Range: coasts and offshore islands of Arnhem Land and Gulf of Carpentaria, from Daly River to Normanton.

E24 ***Pachycephala pectoralis spinicauda*** (Pucheran)

Pteruthius spinicaudus Pucheran, 1853. Voy. Pôle Sud, Zool. **3**, p. 58—l'île Warriors [Torres Str.].

? *Pachycephala salomonis* Oustalet, 1877. Bull. Soc. philom. Paris, 6th ser., **12**, p. 95—des îles Salomon [see p. 207].

Range: (? west coast of Cape York Peninsula), Cape York, islands in Torres Strait and coastal and second-growth formations in southern New Guinea from Merauke eastwards, probably intergrading with E25 near Hall Sound.

E25 ***Pachycephala pectoralis dahli*** Reichenow

? *Pachycephala innominata* Salvadori, 1881. Ornit. Pap. Mol. **2**, p. 222—in Papuasia—ins. Teste (*Ramsay*).

Pachycephala melanura dahli Reichenow, 1897. Orn. Mber. **5**, p. 178—Credner-Inseln, Raluan.

Pachycephala pectoralis neuhausi Stresemann, 1934. Orn. Mber. **42**, p. 24—Sinabiet [Malie].

Pachycephala pectoralis fergussonis Mayr, 1936. Amer. Mus. Novit. No. 869, p. 2—Fergusson Island, D'Entrecasteaux Archipelago.

Range: (a) ? south-eastern New Guinea, from Hall Sound to Milne Bay, (b) ? Teste Island, (c) Fergusson Island, (d) Long Island, (e) Witu Islands, (f) islands in Bungula Bay, New Britain, (g) Talele, Vatom, Duke of York and Credner (Palikuru) Islands, and shores of Blanche Bay, New Britain, (h) Nusa Island (off Kavieng, New Ireland), (j) Malie Island, Lihir group, (k) Nissan Island.

E26 ***Pachycephala pectoralis whitneyi*** Hartert

Pachycephala pectoralis whitneyi Hartert, 1929. Amer. Mus. Novit. No. 364, p. 14—Whitney Island [type designation and discussion attached in error to *Pachycephala implicata*].

Range: Whitney, Momalufu and Akiki Islands, east of Shortland—variable hybrid population between E25 and C9. Related populations, or pure populations of E25, may remain to be discovered elsewhere in the northern Solomons (see p. 208).

E27 ***Pachycephala pectoralis balim*** Rand

Pachycephala pectoralis balim Rand, 1940. Amer. Mus. Novit. No. 1072, p. 8—Balim River, altitude 1,600 meters ; Snow Mts., Netherland New Guinea.

Range : second growth in the Balim and Bele Valleys, northern slopes of Mount Wilhelmina.

F28 ***Pachycephala pectoralis fuliginosa*** Vigors & Horsfield

[*Pachycephala*] *fuliginosa* Vigors & Horsfield, 1827. Trans Linn. Soc. Lond. **15**, p. 241—South coast of New Holland [Port Lincoln, according to Mathews, 1920, p. 208].

Pachycephala occidentalis Ramsay, 1878. Proc. Linn. Soc. N.S.W. **2**, p. 212—Western Australia [Albany, according to Mathews, 1920, p. 209].

Range : (a) south-western Australia, west of a line through Geraldton, the Wongan Hills, Lake Grace and Esperance, (b) South Australia (Eyre and Fleurieu Peninsulas and Kangaroo Island), intergrading via (c) Victorian mallee with F30a.

F29 ***Pachycephala pectoralis glaucura*** Gould

Pachycephala glaucura Gould, 1845. Birds of Australia, **2**, part 18, p. 65—Van Diemen's Land and the islands in Bass's Straits.

Range : Tasmania (except the forests of the south-west) and islands in Bass Straits.

F30 ***Pachycephala pectoralis pectoralis*** (Latham)

Muscicapa pectoralis Latham, 1801. Index Orn. Suppl., p. 51—Nova Hollandia [Port Jackson, according to Mathews 1920, p. 208].

Pachycephala gutturalis youngi Mathews, 1912. Novit. zool. **18**, p. 313—Victoria [Lal Lal, according to Mathews 1920, p. 209].

Range : (a) Victoria east of a line from Heytsbury to Castlemaine, probably intergrading with (b) New South Wales. The range extends west of the Great Dividing Range into the Riverina district of southern New South Wales. Probably confined to eucalyptus forest, and riverine forest in savannah woodland.

F31 ***Pachycephala pectoralis queenslandica*** Reichenow

Pachycephala queenslandica Reichenow, 1899. Orn. Mber. **7**, p. 8—Nord Queensland [Bellenden Kerr, according to Mathews, 1920, p. 209].

Pachycephala gutturalis ashbyi Mathews, 1912. Novit. zool. **18**, p. 313—South Queensland [Blackall Ranges, according to Mathews, 1920, p. 209].

Range : (a) extreme north-eastern New South Wales (Richmond River) and southern Queensland (north to Mackay and Whitsunday Island), (b) Cairns district. Probably confined to rain forest.

F32 ***Pachycephala pectoralis contempta*** Hartert

Pachycephala contempta Hartert, 1898. Bull. B.O.C. 8, p. 15—Lord Howe Island.

Range: Lord Howe.

F33 ***Pachycephala pectoralis xanthoprocta*** Gould

Pachycephala xanthoprocta Gould, 1837. Proc. zool. Soc. Lond., p. 149—in Novâ Cambriâ Australi, apud oram orientalem [error for Norfolk Island according to Mathews, 1928, Birds of Norfolk & Lord Howe Islands, p. 40].

Range: Norfolk Island.

G34 ***Pachycephala* [*pectoralis*] *caledonica*** (Gmelin)—see p. 174.

Muscicapa caledonica Gmelin, 1789. Syst. Nat. **1**, p. 944—nova Caledonia.

Eopsaltria variegata Gray, 1859. Proc. zool. Soc. Lond. part 27, p. 162—Island of Nu.

Pachycephala morariensis Verreaux & des Murs, 1860. Rev. Mag. Zool. p. 393—[le] camp de Morari [New Caledonia].

Range: New Caledonia and Isle of Pines.

G35 ***Pachycephala pectoralis littayei*** Layard

Pachycephala Littayei Layard, 1878. Ann. Mag. nat. Hist. 5th ser., **1**, p. 375—Lifu, New Caledonia [!].

Range: Lifu and Uvea, Loyalty Islands.

G36 ***Pachycephala pectoralis cucullata*** (Gray)

Eopsaltria cucullata Gray, 1859. Cat. Birds Trop. Is. Pacific, p. 21—New Hebrides (Aneitum).

Range: Aneitum.

G37 ***Pachycephala pectoralis chlorura*** Gray

Pachycephala chlorurus Gray, 1859. Cat. Birds Trop. Is. Pacific, p. 20—New Hebrides (Erromango, Aneiteum) [restricted to Erromango by Mayr, 1932*b*, p. 3].

Pachycephala intacta Sharpe, 1900. Ibis, 7th ser., **6**, p. 343—Sandwich Bay, Mallicollo.

Pachycephala pectoralis brunneipectus Mayr, 1932. Amer. Mus. Novit. No. 531, p. 4—Epi Island.

Pachycephala pectoralis banksiana Mayr, 1932. Amer. Mus. Novit. No. 531, p. 6—Vanua Lava, Banks Islands.

Pachycephala pectoralis efatensis Mayr, 1938. Amer. Mus. Novit. No. 986, p. 2—Efate Island, New Hebrides.

Range: New Hebrides and Banks Islands, north of Tanna: (a) Erromango, (b) Efate and Nguna, (c) Mai, Tongariki, Epi, Lopevi, Pauuma and Ambrym, (d) Malekula, Malo, Espiritu Santo, and Dolphin Island, intergrading through (e) Omba, Raga and Maewo with (f) Gaua, Vanua Lava and Ureparapara.

G38 ***Pachycephala pectoralis vanikorensis*** Oustalet

P[achycephala] vanikorensis Oustalet, 1877. Bull. Soc. philom. Paris, 6th ser., **12**, p. 95—l'île Vanikoro.

Range : Vanikoro.

H39 ***Pachycephala pectoralis calliope*** Bonaparte

Pachycephala calliope Bonaparte, 1850. Conspic. Gen. Av. **1**, p. 328—Timor.
Pachycephala melanura arthuri Hartert, 1906. Novit. zool. **13**, p. 299—Wetter.

Range : (a) Timor and Samau, (b) Wetar.

H40 ***Pachycephala pectoralis sharpei*** Meyer

Pachycephala Sharpei Meyer, 1884. S.B. Isis Dresden, Jahr 1884, Abhandl., p. 36—ins. Babbar.

Range : Babar.

H41 ***Pachycephala pectoralis dammeriana*** Hartert

Pachycephala melanura dammeriana Hartert, 1900. Novit. zool. **7**, p. 17—Dammer Island.

Range : Damar.

H42 ***Pachycephala pectoralis fuscoflava*** Sclater

Pachycephala fuscoflava Sclater, 1883. Proc. zool. Soc. Lond. p. 198—Larat, ins. Tenimberensem.

Range : Tenimber Islands.

H43 ***Pachycephala pectoralis macrorhyncha*** Strickland

Pachycephala macrorhyncha Strickland, 1849. Contr. Orn. (Jardine), p. 91—Amboina.
Pachycephala macrorhyncha alfurorum Stresemann, 1914. Novit. Zool. **21**, p. 132—Gunung Sofia (Mittel-Seran).

Range : (a) Ceram, (b) Amboina.

H44 ***Pachycephala pectoralis buruensis*** Hartert

Pachycephala melanura buruensis Hartert, 1899. Bull. Brit. orn. Cl. **8**, p. 32—Buru.

Range : Buru.

H45 ***Pachycephala pectoralis clio*** Wallace

Pachycephala clio Wallace, 1862. Proc. zool. Soc. Lond., p. 341—Sula and Buru [restricted to the Sula Islands by Hartert, 1899. Bull. Brit. orn. Cl. **8**, p. 33].

Range : Sula Islands

H46 ***Pachycephala pectoralis pelengensis*** Neumann

Pachycephala melanura pelengensis Neumann, 1941. Zoöl. Meded. **23**, p. 112—Peleng.

Range : Peleng and Banggai Islands.

H47 ***Pachycephala pectoralis collaris*** Ramsay

Pachycephala collaris Ramsay, 1878. Proc. Linn. Soc. N.S.W. **3**, p. 74—Courtance Island, South-East coast, New Guinea ; *tom. cit.*, p. 281—Teste Island [see p. 206].

Pachycephala rosseliana Hartert, 1898. Bull. Brit. orn. Cl., **8**, p. 8—Rossel Island.

Pachycephala pectoralis misimae Rothschild & Hartert, 1918. Novit. zool. **25**, p. 311—St. Aignan or Misima Island.

Range : (a) Conflict, Begum and Egum groups (and Coutance or Teste Islands?), intergrading through (b) Misima and the Deboyne group with (c) Rossel.

H48 ***Pachycephala pectoralis citreogaster*** Ramsay

? *Saxicola merula* Lesson, 1828. Voy. Coquille (Duperry) Zool. **1**, pt. 2, p. 662—la Nouvelle-Irlande, aux environs du Port Praslin [see p. 209].

Pachycephala citreogaster Ramsay, 1876. Proc. Linn. Soc. N.S.W. **1** p, 66—New Britain and adjacent islands.

Pachycephala pectoralis sexuvaria Rothschild & Hartert, 1924. Bull. Brit. orn. Cl. **44**, p. 50—St. Matthias Island (Mussau).

Range : (a) Umboi and New Britain, (b) New Ireland and Feni, (c) Lavongai, (d) Mussau.

H49 ***Pachycephala pectoralis ottomeyeri*** Stresemann

Pachycephala pectoralis ottomeyeri Stresemann, 1933. Orn. Mber. **41**, p. 116—Komat auf Lihir.

Range : Lihir Island.

H50 ***Pachycephala pectoralis tabarensis*** Mayr

Pachycephala pectoralis tabarensis Mayr, 1955. Amer. Mus. Novit., No. 1707, p. 35—Tabar Island, Tabar group.

Range : Tabar Island.

H51 ***Pachycephala pectoralis goodsoni*** Rothschild & Hartert

Pachycephala pectoralis goodsoni Rothschild & Hartert, 1914. Novit. zool. **21**, p. 296—Manus.

Range : Manus.

H52 ***Pachycephala pectoralis ornata*** Mayr

Pachycephala pectoralis ornata Mayr, 1932. Amer. Mus. Novit. No. 531, p. 8—Santa Cruz [Ndeni], Santa Cruz Islands.

[*Pachycephala*] *atrata* Mayr, 1932. Amer. Mus. Novit. No. 531, p. 10—*nomen nudum* [used by Mayr in MS.].

Range: (a) Ndeni, (b) Reef, Duff and Swallow groups.

H53 ***Pachycephala pectoralis utupuae*** Mayr

Pachycephala pectoralis utupuae Mayr, 1932. Amer. Mus. Novit. No. 531, p. 8—Utupua, Santa Cruz Islands.

Range: Utupua.

H54 ***Pachycephala pectoralis kandavensis*** Ramsay

Pachycephala kandavensis Ramsay, 1876. Proc. Linn. Soc. N.S.W. **1**, p. 65—" Kandavu ".

Range: Kandavu group and Mbengha.

H55 ***Pachycephala pectoralis vitiensis*** Gray

Pachycephala vitiensis Gray, 1859. Cat. Birds Trop. Is. Pacific, p. 20—Feejee Islands (Island of Ngau).

Range: Ngau.

H56 ***Pachycephala pectoralis lauana*** Mayr

Pachycephala pectoralis lauana Mayr, 1932. Amer. Mus. Novit. No. 531, p. 12—Ongea Levu Island, Lau Archipelago, Fiji Islands.

Range: Ongea Levu, Fulanga and Wangava, southern Lau Archipelago.

H57 ***Pachycephala pectoralis melanops*** (Pucheran)

Eopsaltria melanops Pucheran, 1853. Voy. Pôle Sud., Zool. **3**, p. 56—Vavao.

Range: Vavau group and Late, Tonga.

PACHYCEPHALA FLAVIFRONS (Peale)

Eopsaltria flavifrons Peale, 1848. U.S. Explor. Exped. Birds (subsequently withdrawn), p. 96—Upolu.

Range: Upolu and Savai, Samoa.

Subspecies to be recognised according to current usage

Subspecies which are distinguished from one another by measurements alone, and which are near the borderline of subspecific distinctness under the seventy-five percent rule, are bracketed together and the junior name indicated by an asterisk.

Pachycephala schlegelii :
1 *schlegelii*
2 *cyclopum*
3 *obscurior*

Pachycephala soror :
1 *soror*
2 *klossi*
3 *bartoni*

Pachycephala pectoralis :
A1 *fulviventris*
A2 *javana*
A3a *fulvotincta*
A3b *jubilarii**
A4 *everetti*
A5 *teysmanni*
B6 *mentalis*
B7 *tidorensis*
B8 *obiensis*
C9 *bougainvillei*
C10a–b *orioloides*
C10c *pavuvu*
C11 *cinnamomea*
C12 *sanfordi*
C13 *melanonota*
C14 *melanoptera*
C15 *centralis*
C16 *feminina*
C17 *christophori*
D18a *graeffii*
D18b *optata*
D19 *aurantiiventris*
D20a *torquata*
D20b *koroana*
D21 *bella*
E22a *bynoei*
E22b–c *melanura*
E22d *hilli*
E23 *violetae*
E24 *spinicauda*
E25c *fergussonis**
E25d–j *dahli*
E26 *whitneyi*
E27 *balim*
F28a *occidentalis*
F28b–c *fuliginosa*
F29 *glaucura*
F30a *youngi*
F30b *pectoralis*
F31a *ashbyi*
F31b *queenslandica*
F32 *contempta*
F33 *xanthoprocta*
G34 *caledonica*
G35 *littayei*
G36 *cucullata*
G37a *chlorura*
G37b–f *intacta*
G38 *vanikorensis*
H39a *calliope*
H39b *arthuri*
H40 *sharpei*
H41 *dammeriana*
H42 *fuscoflava*
H43a *alfurorum**
H43b *macrorhyncha*
H44 *buruensis*
H45 *clio*
H46 *pelengensis*
H47a–b *collaris*
H47c *rosseliana*
H48a–c *citreogaster*
H48d *sexuvaria*
H49 *ottomeyeri*
H50 *tabarensis*
H51 *goodsoni*
H52 *ornata*
H53 *utupuae*
H54 *kandavensis*
H55 *vitiensis*
H56 *lauana*
H57 *melanops*

NOTES

Pachycephala schlegelii viridipectus Hartert & Paludan (3b)

The differences between *viridipectus* and *obscurior* 3a are too slight for subspecific separation (cf. Mayr, *in litt.*), besides which they intergrade smoothly (Mayr & Gilliard, 1954).

Pachycephala pectoralis jubilarii Rensch (A3b)

From a study of A.M.N.H. material, Mayr (*in litt.*) concludes that the size difference between *jubilarii* and *fulvotincta* A3a is sufficient for subspecific separation.

Pachycephala pectoralis atromaculata Meise (= A4)

Mayr (*in litt.*) finds no difference in colour between *atromaculata* and *everetti*, and my few measurements suggest no size difference adequate for separation.

Pachycephala pectoralis gilolonis Kuroda (= B6).

Mayr (*in litt.*) finds no difference between *gilolonis* and *mentalis*.

Pachycephala pectoralis ambigua Mayr (D19c)

The undesirability of recognizing two variable hybrid subspecies (*ambigua* and *torquata* D20a) between *aurantiiventris* D19a and *koroana* D20b has been discussed (p. 176). Since *ambigua* intergrades smoothly with *aurantiiventris* it seems best to combine them, although the end populations are very distinct.

Female of **bynoei** (E22a)

There are four females from Cossack in the White Collection of the National Museum of Victoria. Although no comparative material of *melanura* E22c was available, these appeared to agree well with the female of that form. The desirability of a comparative description has been pointed out to the Museum authorities.

Intergradation of **spinicauda** *(E24) with* **dahli** *(E25)*

A single female from Dalena, Hall Sound (A.M.N.H. Reg. No. 329999) differs from typical *spinicauda* females, and approaches those of *dahli*, in having the underparts much yellower and less ochraceous (cf. Rand, 1940).

The subspecies on Teste Island

Ramsay (1878*a*, 74) described *Pachycephala collaris* (H47a) from Cou(r)tance Island, off the coast of south-eastern New Guinea. Later (1878b, 281) he recorded *P. melanura* (= *spinicauda* E24) on Coutance, and gave the locality of *collaris* (without further comment) as Teste Island, off the extreme south-eastern tip of New Guinea. He further described from Teste a form which Salvadori later (1881, 222) named *P. innominata* (? E25b) from this description. The single specimen is described as having an ashy-grey tail and slaty-black occiput, and the yellow collar " intercepted on the head and neck ".

The type of *collaris* and the female described by Ramsay are in the British Museum (Natural History), Reg. Nos. 95.12.24.2 & 4 respectively. Neither bears a field label, but both are reputedly from Coutance. Two males (B.M.(N.H.) Nos. 78.10.19.5 & 6) bear field labels giving their locality as Teste, and No 6 is recorded as collected by G. W. Baiston Ingham, one of the collectors mentioned by Ramsay (1878*b*, 241). These specimens agree well with males of *spinicauda*, *fergussonis* and *dahli* E24 & 25c–k.

There are no further specimens of *P. pectoralis* from Teste or Coutance Islands in the B.M.(N.H.), the A.M.N.H., or the Australian Museum. It seems most probable that both are inhabited by black-tailed forms of group E., and that the lost type of *innominata* was a specimen moulting into adult plumage. Conceivably Ramsay's notorious unreliability over localities extends in this instance to the description, and " ashy-grey " should refer to the wings. *P. innominata* Salvadori must be considered unidentifiable. The type locality of *collaris* remains to be determined. For the present it seems best to accept the evidence of the original description, and the label of the type, giving the locality as Coutance.

Pachycephala pectoralis fergussonis Mayr (E25c)

The two known specimens of *fergussonis* are distinctly larger than typical *dahli*, and slightly deeper yellow beneath. However, *dahli* from Long Island E25d (and Teste E25b ?) approach them in size. In view of the geographical variation in size within *dahli*, and the slightness of the colour difference, it is best to submerge *fergussonis* in *dahli* until females are available for comparison (cf. Mayr, *in litt.*).

Pachycephala salomonis Oustalet. (? = E24)

The locality of the single (male) specimen was given (Oustalet 1877, 95) as the Solomon Islands, although d'Urville's " Voyage au Pôle Sud " in the " *Astrolabe* " and " *Zélée* " did not stop there. From an examination of the type by Professor Berlioz, Mayr (1932*a*, 21) concluded that *salomonis* is a synonym of *dahli* Reichenow, 1897 (E25), but that (owing to the unreliability of the locality and the heterogynism of closely related races) it must be considered unidentifiable. Comparison of the type with males of *dahli*, *spinicauda* and *citreogaster*, kindly undertaken by Professor Berlioz, confirms that it is inseparable from those of the *violetae-spinicauda-dahli* aggregate E23–25, and quite different from *citreogaster* H48. Mayr (1955, 34, and *in litt.*) supposes the type to have been collected at Port Praslin, New Ireland, and the name therefore to be a synonym of *citreogaster*. This error springs from that (Mayr, 1932*a*) of supposing that the type was collected on D'Urville's earlier " Voyage de *l'Astrolabe* ", which called at Port Praslin.

Even if the locality of *salomonis* were known, the principle of conservation (Copenhagen Decisions, 1953, 25) would debar the use of the name, since it seems not to have been used since its publication. From the itinerary of the voyage it seems most probable that the type was collected at Port Essington (*violetae* E23) or the Torres Strait (*spinicauda* E24), where the vessels actually called ; though it might have been brought by canoe from Teste Island or Nissan (*dahli* E25), or even from somewhere in the northern Solomons (cf. *whitneyi* E26 ?). In the circumstances, *P. salomonis* must be considered unidentifiable.

*White-throated **Pachycephala** in the Solomons*

Besides the hybrid race *whitneyi* E26 on small islands west of Shortland, there are indications that other populations related to *dahli* E25 may remain to be discovered in the northern Solomons. Hartert (1926, 46) records a specimen from Munia, south-west of Fauro in the Bougainville Strait. A male (B.M.(N.H.) Reg. No. 36.4.20.14) collected on or near Buka (Moyne-Chaplin, 22nd December, 1935) agrees well with *dahli* and with white-throated males of *whitneyi*, except that it has a small black chin-spot.

Pachycephala pectoralis brunneipectus, banksiana and ***efatensis*** Mayr (G37c, f & b)

Though separable in long series of females from different islands, all the populations from Efate to the Banks Islands G37b–f should be combined in *intacta* Sharpe (cf. Mayr, *in litt.*).

Pachycephala macrorhyncha alfurorum Stresemann (H43a)

The size difference between *alfurorum* and *macrorhyncha* H43b seems to be sufficient for subspecific separation (Mayr, *in litt.*), as my measurements tend to confirm.

Pachycephala collaris Ramsay (H47a)

In view of the uncertainty about the type locality of *collaris* (p. 206), Professor Mayr has suggested that a redescription of the original specimens may be useful.

The following descriptions must be read in conjunction with those of the standard patterns (p. 138). Colours are cited according to the code of Villalobos-Dominguez & Villalobos (1947). The type was compared with two males of *misimae* H47b from Misima (B.M.(N.H.) Nos. 99.5.20.6 & 7) and one of *rosseliana* H47c (1917.11.21.1); Ramsay's female with two of *misimae* from Misima (99.5.17.43 and 99.5.20.5). Unfortunately, they were not critically compared with a male of *collaris* from East Island, nor a female of *rosseliana*, both borrowed from the American Museum of Natural History.

ADULT MALE. Type (B.M.(N.H.) Reg. No. 1895.12.24.2).

Throat-feathers with little or no grey at bases (as *misimae* and *rosseliana*).

Underparts about OOY/OY.17.12°: *misimae* similar, *rosseliana* a little more golden, towards OOY.

Underside of tail a little more olivaceous, less fuscous, than in *rosseliana*, *misimae* intermediate.

Collar somewhat washed with brownish-olive on hind-neck: in *rosseliana*, much narrower and quite olivaceous on hind-neck, *misimae* intermediate.

Mid-back about YYO.5.12°: *rosseliana* darker and greener, about YYO/Y.3.12°, *misimae* paler and slightly greener, about YYO(Y).7.12°.

Edges of remiges (worn) greyer, edges of upper wing-coverts yellower, centres of wing-feathers paler than in *rosseliana*—*misimae* agrees with *collaris*.

Tail (only 5 rectrices remain) yellowish olive, central rectrices without black; remainder with vague brown patches (somewhat broken up into transverse bars) subterminally on inner webs; shafts brown, paling basally. In *misimae* central rectrices have vague brownish barring; remainder have blackish brown patches occupying most of the inner webs; shafts darker brown. In *rosseliana*, central rectrices are dark olive with long blackish patches along the shafts on the inner webs; remainder are brownish black with dull olive edges (widest towards the bases of the outer webs); shafts black, becoming dark brown basally,

In *rosseliana* only, the rump, upper tail-coverts and tail are somewhat washed with brown.

ADULT FEMALE. (95.12.24.4).

Throat white with brownish fringing (as in *misimae*).

Gorget narrow, pale and vaguely-defined, vinous grey in colour (about SO.16.2°) as in 99.5.20.5 of *misimae*; in 99.5.17.43 it is wider, deeper, more sharply defined beneath and browner (about OOS.12.4°).

Underparts rich yellow, about OY.17.12° on mid-belly, with lower breast and flanks somewhat olivaceous to brownish; 99.5.17.43 agrees; 99.5.20.5 is much paler, about OY.18.10° on mid-belly.

Upperparts very brown, as in 99.5.17.43 (crown about OOS.6.5°, mid-back about O.4.12°); 99.5.20.5 is much less brown, with crown greyer (about OOS.5.3°) and mantle greener (about YYO.4.10°).

Edges of wing-feathers slightly greyer, less rufous, than in *misimae*.

Tail intermediate between 99.5.17.43 (browner) and 99.5.20.5 (greener).

Pachycephala pectoralis misimae Rothschild & Hartert (H47b)

Although it shows signs of gene-flow from *rosseliana* H47c, this form is nearest to *collaris* H47a, with which it should be combined (cf. Mayr, *in litt.*).

Saxicola merula Lesson (? = H48b)

The locality of the type, a juvenile, was given by Lesson as Port Praslin, on the south-east coast of New Ireland. This would make the name the senior synonym of *citreogaster*, though the principle of conservation would require its suppression. But many specimens brought back by French expeditions of the late eighteenth and early nineteenth centuries are wrongly localized, and several species recorded from Port Praslin do not in fact occur in the Bismarcks (Mayr, *in litt.*). Salvadori (1881, 219) questioned the locality, pointing out the resemblance of the type to juveniles of *macrorhyncha* (Amboina H43b). Juveniles of *citreogaster* and *macrorhyncha* probably cannot be separated with certainty, and Mayr, who has examined the type, considers it to be unidentifiable.

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Dr. A. J. Cain introduced me to the principles and methods of systematics, suggested the study of *Pachycephala pectoralis* and the research on geographical variation of which it forms a part, and has been a constant source of advice. Professor Ernst Mayr has greatly encouraged me in the study of a group on which he is the authority, and liberally made me free of his knowledge and experience : my indebtedness to his published and unpublished work will be evident throughout the text of this paper. Dr. Dean Amadon has been to great trouble to answer a list of queries from the material in the American Museum of Natural History. Professor Jean Berlioz has been most helpful in comparing the type of *Pachycephala salomonis*, and discussing the nomenclatural problem. Dr. Allen Keast has unsuccessfully sought the type of *Pachycephala innominata* in the Australian Museum. Dr. Cain, Professor Mayr, Mr. R. E. Moreau and Dr. H. W. Parker have read drafts of this paper at various stages, and made invaluable criticisms and suggestions. Mr. H. O. Ricketts has carefully checked the final draft, detecting many lapses and obscurities, and helped me in proof-reading. Mr. R. J. Drumm, O.B.E., has greatly helped in seeing the paper through the press. Both the British Museum (Natural History) and the American Museum of Natural History have allowed me to borrow many specimens. The paper was prepared between 1952 and 1955, at the Department of Zoology and Comparative Anatomy, University of Oxford, under Professor A. C. Hardy, F.R.S. Working facilities were also granted at the Edward Grey Institute of Field Ornithology by Dr. David Lack, F.R.S., and at the Bird Room of the British Museum (Natural History) by Mr. J. D. Macdonald. Professor Hardy and the Department of Scientific and Industrial Research gave financial assistance during the preparation of the paper, and field work in the Solomons was financially supported by the Percy Sladen Trustees and the Parliamentary Grants Committee of the Royal Society.

MEASUREMENTS

In addition to my own measurements, Professor Mayr has most kindly put at my disposal most of those taken by himself (for Mayr, 1931*b*, *c*; 1932*a*, *b*; 1936, 1938, 1941*a*, 1944*c* and 1955) and by Mrs. Kate Jennings (for Mayr, 1954*a*). Several specimens were measured both by Mayr or Jennings and by myself, while I measured many others twice. The distributions of the discrepancies (between Mayr's and Jennings' and my own first measurements on the one hand, and my definitive series on the other) indicate to what extent these results are comparable or repeatable.

Wing :	self$_2$—Mayr	mean	− 0·07 mm.,	s.d.	± 1·20 mm.	(27 measurements)
	self$_2$—Jennings	,,	− 0·18 ,,	,,	± 0·95 ,,	(14 ,,)
	self$_2$—self$_1$	,,	+ 0·40 ,,	,,	± 0·24 ,,	(148 ,,)
Tail :	self$_2$—Mayr	,,	+ 0·25 ,,	,,	± 0·98 ,,	(26 ,,)
	self$_2$—Jennings	,,	+ 0·08 ,,	,,	± 2·11 ,,	(15 ,,)
	self$_2$—self$_1$	,,	− 0·41 ,,	,,	± 0·51 ,,	(148 ,,)

Although several individual discrepancies exceed 2 mm., the mean discrepancies are small. However, several of the standard deviations differ to a high degree of significance (by the variance-ratio test), and it seems unwise to combine Mayr's and Jennings' series with my own. I have inserted them at the appropriate points in the table, prefixed by M or J respectively. Asterisks indicate measurements in my series which appear also in Mayr's or Jennings'. Since weight determinations are not subject to the same personal bias, I have combined our series for C17a. Weights for C11 were taken by Cain and myself, the remainder by the Whitney Expedition of the American Museum of Natural History.

Series of five measurements or less are given in full, with replications indicated in parenthesis—e.g. 76, 78·5, 80(2), 81·5. Longer series are summarized in the form *mean ± standard deviation* (*number in series*)—e.g. 86·8 ± 2·10 (13).

Recognizably distinct populations are distinguished in the tables by their ciphers, and by subspecies names (not all of which are admitted on p. 205) where appropriate. Weights and wing and tail lengths are given separately for adult males and females. The sexing of Mayr's specimens, those of the O.U.(D.Z.) Solomons Expedition (C11 & 17a), and the hen-feathered series C16 and F33 have been accepted for this purpose. However, much of the remaining material is not sexed, and some determinations are questionable. Therefore only specimens showing feathers belonging to the adult male plumage have been taken as adult males ; and only those sexed as females and showing female plumage, without male or juvenile feathers, as adult females.

In the few forms of which I had adequate series of males, females and juveniles, reliably sexed, there was little indication of significant and constant differences between sex and age groups, in the measurements of bills and tarsi (values for C17a are analysed on p. 218). I have therefore risked the introduction of some bias, in order to have longer series, by combining the measurements of all specimens except nestlings. Mayr's raw data contain very few individual measurements of bills and none of tarsi, and I have not repeated the indications of size range published in the papers cited.

Weight in grams

My measurements taken to the nearest 0·5 gm., with a long-scale spring balance (Gibb balance), calibrated in the field.

	Males	Females
C10a *orioloides*	49·9 ± 2·62 (17)	42, 44, 50
C11 *cinnamomea*	51·5 ± 2·24 (19)	44·9 ± 1·81 (8)
C12 *sanfordi*	51·3 ± 2·25 (18)	49·5 ± 2·00 (19)
C17a *christophori*	33·5 ± 2·96 (45)	32·1 ± 2·36 (20)
C17b ,,	34, 35 (2)	—
E25k *dahli*	29·0 ± 1·69 (8)	27, 28, 29

Wing and tail lengths, in millimetres (pp. 212–216)

My wing lengths taken to nearest 0·5 mm., from wing-bend to tip of longest primary (of left wing wherever possible), with wing pressed flat.

My tail lengths taken to nearest 0·5 mm., from tip of longer central quill to insertion of central quills in common sheath.

Tarsus and culmen lengths, and bill depth, in millimetres (pp. 217–219)

My tarsus lengths taken to nearest 0·5 mm., along outer side of tarsus, from groove of intertarsal joint to eminence near plantar angle of hind toe.

My culmen lengths taken to nearest 0·5 mm., chordwise, from tip to angle of culmen with skull.

My bill depths taken to nearest 0·5 mm., perpendicular to tomium at hind edge of nostril, from culmen to lower edge of mandible (bill fully closed).

			Wing		Tail	
			Male	Female	Male	Female
	P. schlegelii					
1	*schlegelii*		84·5	80·5	59·5	60·5
2	*cyclopum*		90	88	69	—
3a	*viridipectus*		84·5 ± 2·67 (12)	82, 84	61·7 ± 1·71 (10)	60·5, 63·5
3b	*obscurior*		86·9 ± 2·12 (13)	82, 83, 86	65·7 ± 2·19 (13)	59·5, 67
	P. soror					
1	*soror*		90, 92	82, 82·5, 88·5	66	63, 64, 65
2	*klossi*		90·3 ± 1·76 (9)	87, 87·5	60·2 ± 1·61 (10)	58
3	*bartoni*		87·4 ± 1·66 (11)	86·2 ± 1·71 (7)	60·9 ± 2·44 (11)	61·8 ± 2·38 (7)
	P. pectoralis					
A1	*fulviventris*		82, 83, 86	80, 82, 82·5, 84, 87	58, 61, 62	59, 61, 62
		M	84·5 ± 1·67 (10)	83·4 ± 1·96 (8)	59, 60, 61, 64	—
A2a	*javana*		84·5	83	—	64
A3a	*fulvotincta*		76, 78·5, 80 (2), 81·5	78·5 (2)	57, 57·5, 58 (3)	—
A3b	*jubilarii*		79·5, 80·5, 81·5	81·5	59·5, 60, 62	63
A4	*everetti*		81 (2), 81·5, 83	77·5	61, 63·5, 64, 67·5	62·5
A5	*teysmanni*		75·5	73·5	60·5	55
B6	*mentalis*		88, 90, 90·5, 92, 94	83, 89·5, 90, 90·5	61·5, 64 (2), 64·5, 65·5	63, 63·5, 65, 65·5
B7	*tidorensis*		97·5, 99, 99·5 (2)	93·5, 94	71, 72, 75	66·5, 72·5
			99·3 ± 0·21 (6)[1]	—	70 (3), 71·5, 74[1]	—
B8	*obiensis*		95, 95·5, 97 (2)	97	68, 69, 69·5, 74·5	70
C9	*bougainvillei*		97·5 (2)	96, 100·5	69·5, 72·5	71·5, 73
		M	103·2 ± 2·31 (25)	98·6 ± 1·85 (12)	72·9 ± 2·42 (24)	69, 72
C10a	*orioloides*		100	96·5	72	69·5
		M	102·9 ± 1·98 (26)	98·6 ± 1·85 (12)	71·8 ± 1·85 (25)	69·8 ± 2·30 (13)
C10b	,,		104	—	73	—
		M	106·3 ± 2·76 (15)	99·1 ± 3·36 (9)	74·8 ± 2·54 (13)	69·6 ± 2·96 (9)

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[1] Wrongly or inadequately localized specimens, separated from *mentalis* (type (♂): wing 90·5, tail 64) on measurements.

		Wing		Tail	
		Male	Female	Male	Female
C10c *pavuvu*		107·5	99	74	68
	M	105·9 ± 1·35 (13)	100·8 ± 1·14 (13)	71·5 ± 1·45 (14)	67·9 ± 1·44 (12)
C11 *cinnamomea*		103·5 ± 1·77 (17)	98·5 ± 2·81 (11)	76·2 ± 1·64 (16)	74·6 ± 2·19 (12)
	M	105·4 ± 2·01 (19)	100·0 ± 2·61 (7)	77·9 ± 1·94 (19)	74·0 ± 1·63 (7)
C12 *sanfordi*		104*	100*	75*	73·5*
	M	103·3 ± 2·20 (17)	99·7 ± 1·59 (18)	75·4 ± 1·62 (12)	72·9 ± 1·63 (16)
C13a *melanonota*		99	103	68	68
	M	98·0 ± 2·08 (7)	96 (3), 98	66 (2), 68, 69, 72	68 (2), 69
C13b ,,	M	98·4 ± 2·24 (14)	93	69·9 ± 2·40 (14)	68
C14 *melanoptera*		104*	100·5*	69·5*	71·5*
	M	105·3 ± 2·12 (25)	97, 98, 99, 101	74·0 ± 2·55 (26)	68, 69, 72 (2)
C15 *centralis*		95·5*	—	68·5*	—
	M	95·7 ± 2·39 (64)	92·3 ± 2·06 (18)	68·9 ± 2·30 (59)	66·9 ± 1·93 (18)
C16 *feminina*		85, 86·5, 93·5*	84·5*, 85	54·5, 60·5, 63*	53·5*, 54·5
	M	86·3 ± 2·85 (15)	84·8 ± 2·78 (7)	55·9 ± 2·83 (15)	54·4 ± 2·07 (7)
C17a *christophori*		85·9 ± 2·23 (41)	84·5 ± 2·32 (18)	59·6 ± 1·87 (35)	60·1 ± 1·95 (11)
	M	87·8 ± 0·83 (12)	86·1 ± 1·95 (7)	60·2 ± 2·58 (10)	59·4 ± 1·52 (7)
C17b ,,	M	88·5 ± 1·05 (6)	85·7 ± 1·67 (8)	58·7 ± 1·03 (6)	56·8 ± 1·58 (8)
D18a *graeffii*		91, 94, 95·5, 97·5	90·5	65·5, 68·5, 69, 73	65
	M	95·0 ± 2·29 (20)	92·75 ± 1·36 (8)	67·1 ± 2·08 (20)	65·2 ± 1·58 (8)
D18b *optata*		92·2 ± 2·45 (6)	90·5	65·5 ± 2·44 (6)	65
	M	92·7 ± 0·52 (6)	92, 93	67·0 ± 2·10 (6)	63, 64, 66
D19a *aurantiiventris*		88*, 90·5, 91·5, 93*	87	66, 68, 69·5*	66
	M	91·3 ± 1·70 (13)	86 (2), 87	66·2 ± 1·94 (16)	63, 64
D19b/c *ambigua*		92·5*	92·5*	67*	69·5*
	M	92·2 ± 1·92 (9)^2	90·9 ± 0·90 (7)^2	66·4 ± 1·50 (8)^2	65·7 ± 1·51 (6)^2
D20a *torquata*		93·6 ± 1·79 (10)	90, 91·5, 92, 93	65·3 ± 2·32 (8)	64, 64·5, 66·5 (2)
	M	95·6 ± 1·51 (10)	91·9 ± 1·36 (8)	67·1 ± 2·08 (10)	65·3 ± 1·58 (8)
D20b *koroana*		93·5*	91·5*	66*	67·5*
	M	94·7 ± 1·98 (7)	91 (2), 92, 93, 94	68·6 ± 1·40 (7)	66·3 ± 1·22 (6)
D21 *bella*	M	94	91, 92	61	62, 66
E22a *bynoei*	J	81, 85	—	64	—

[2] " Every specimen molting " (Mayr, MS).

		Wing		Tail	
		Male	Female	Male	Female
E22b *melanura*		80*, 81*, 84*	—	59*, 61·5*, 62·5*	—
	J	79·5, 80, 80·5, 81·5, 82	78, 82	59, 59·5, 60, 60·5, 62	59, 65
E22c ,,		82	79·5*	61·5	62*
	J	80·5 ± 1·37 (15)	78·6 ± 2·21 (7)	60·7 ± 1·83 (13)	60·1 ± 1·59 (7)
E22d *hilli*		84·5*	82*	66*	63*
	J	84	83	64	65
E23 *violetae*		85·5*, 86*	84*, 85*	68*	64 (2)*
	J	84·3 ± 1·60 (12)	82·4 ± 1·57 (9)	63·5 ± 2·02 (11)	61·3 ± 1·33 (10)
E24 *spinicauda*		87·1 ± 2·54 (6)	87·5*	63·5 ± 1·93 (7)	67*
		(85·5, 88·5)*		(64, 65·5, 68)*	
	J, M	87·4 ± 2·13 (7)	88	66·2 ± 1·30 (10)	66·5
E25a cf. *dahli*	M	91	91	69	66·5
E25b "*innominata*"		92·5, 93	—	69 (2)	—
E25c *fergussonis*		96*	—	72·5*	—
	M	94·5, 96	—	70·5, 74·5	—
E25d *dahli*		93	90	69	66
E25e ,,		86, 87	83	64, 64·5	67·5
E25g ,,		90·5, 92 (2), 92·5	89, 89·5, 91	63·5, 65, 66, 67	63 (2), 64, 64·5
E25j ,,		—	—	—	63·5
E25k ,,		—	89, 89·5	—	65, 67
	M	91·5 ± 2·00 (8)	88 (2), 89	65·9 ± 1·20 (6)	64 (3)
E26 *whitneyi*		92*, 95*	90*, 90·5*	65*, 66·5*, 69*	65*
	M	95·7 ± 4·00 (8)	90·8 ± 2·63 (9)	66·7 ± 3·20 (8)	66·1 ± 0·99 (8)
E27 *balim*		88	—	68	—
F28a *occidentalis*		98·0 ± 2·10 (12)	91, 94·5, 95	76·9 ± 1·43 (8)	75, 75·5, 78
	J	96·7 ± 2·43 (25)	93·0 ± 1·68 (15)	75·5 ± 2·44 (25)	75·0 ± 2·13 (16)
F28b *fuliginosa*		95, 98 (3)	92·5*, 99·5	75·5 (2), 78, 79	75·5*, 80
	J	97·1 ± 1·73 (12)	94·6 ± 1·40 (8)	75·4 ± 1·43 (11)	73·2 ± 1·39 (9)
F28c ,,	J	94, 95, 97 (2), 98	90·5, 95, 96·5, 97	73, 75·5, 76·5, 77, 78	70·5, 71, 77, 79
F29 *glaucura*		103·0 ± 2·02 (6)	99, 101	83·7 ± 2·28 (6)	78, 79
	J	101·2 ± 1·20 (9)	100·4 ± 2·34 (7)	80·0 ± 1·61 (7)	80·8 ± 3·08 (6)

		Wing		Tail	
		Male	Female	Male	Female
F30a *youngi*		101·5, 102 (2), 102·5	95·5, 97	79·5, 80, 80·5, 81	75, 77
	J	99·3 ± 1·95 (17)	95·1 ± 1·91 (7)	76·5 ± 2·00 (18)	73·8 ± 2·39 (16)
F30b *pectoralis*		95·3 ± 2·64 (6)	96·5	73·4 ± 2·88 (6)	74
	J	96·8 ± 2·00 (15)	95·2 ± 2·87 (11)	73·7 ± 2·50 (15)	74·5 ± 2·77 (11)
F31a *ashbyi*		87·5, 90, 95, 96·5	92	70, 71·5, 74·5 (2)	71
	J	93·2 ± 3·20 (10)	87·5 ± 3·39 (15)	72·5 ± 2·94 (8)	70·8 ± 2·89 (16)
F31b *queenslandica*		88, 90, 92, 94·5	88*	62·5, 64·5, 67·5, 70·5	67*
	J	90·3 ± 2·10 (26)	88·2 ± 0·99 (6)	66·6 ± 2·95 (26)	61, 64, 64·5, 65, 66
F32 *contempta*		93·1 ± 2·39 (8)	86, 90·5	74·1 ± 1·58 (8)	72, 73
F33 *xanthoprocta*		95·9 ± 2·16 (6)	90·5, 92·5, 93, 94·5, 96·5	74·7 ± 1·94 (6)	75·8 ± 1·40 (6)
G34 *caledonica*		82·4 ± 2·48 (6)	81·5, 83·5, 85, 87	65, 66·5, 67, 67·5	64·5, 65·5, 66·5, 70·5
G35 *littayei*		100·5, 101, 101·5	97	71·5, 73	70·5
G36 *cucullata*		86, 87, 87·5, 89	82, 84	63, 64, 64·5, 66·5	58, 62·5
G37a *chlorura*		88·5, 90	—	66 (2)	—
G37b *efatensis*		85·5, 87 (2), 87·5	—	63, 64, 64·5, 66·5	—
G37c *brunneipectus*		—	86·5*	—	65*
	M	86·9 ± 1·28 (17)	86·0 ± 1·66 (9)	65·2 ± 2·13 (18)	65·4 ± 1·43 (9)
G37d *intacta*		84·2 ± 1·62 (9)	82·5	62·6 ± 2·95 (10)	61·5
	M	86·0 ± 1·99 (23)	83·8 ± 1·97 (23)	63·7 ± 2·06 (21)	61·1 ± 1·86 (22)
G37e cf. *banksiana*		—	86·5*	—	66*
	M	87·2 ± 1·36 (12)	84·5 ± 1·92 (6)	64·9 ± 1·49 (17)	63·3 ± 1·60 (7)
G37f *banksiana*		87·5	87·5*	64·5	64*
	M	86·4 ± 1·51 (7)	84·7 ± 1·50 (15)	62·9 ± 0·99 (8)	60·8 ± 1·83 (15)
G38 *vanikorensis*		83*	84*	60*	58*
	M	85·7 ± 0·58 (16)	82·9 ± 0·99 (10)	60·4 ± 1·22 (14)	59·0 ± 1·18 (11)
H39a *calliope*		84, 87·5, 88·5, 89	88	65, 68 (2), 70·5	69·5
	M	90·1 ± 1·83 (11)	87·5, 92·5	68·4 ± 2·42 (10)	67
H39b *arthuri*		91	89	71	72·5
H40 *sharpei*		90	88, 90·5	64·5	66·5
H41 *dammeriana*		91	83	—	71·5

		Wing		Tail	
		Male	Female	Male	Female
H42 *fuscoflava*		109·5	101·5, 103	79·5	71·5
H43a *alfurorum*		89·5, 90·5, 92, 93, 94	89·5	62, 65, 67, 67·5, 68	66
H43b *macrorhyncha*		95·9 ± 1·32 (9)	88·5, 90·5 (3), 92	68·6 ± 1·06 (9)	65 (2), 66, 66·5, 68
H44 *buruensis*		92·6 ± 1·79 (9)	87·7 ± 2·52 (7)	67·6 ± 1·99 (9)	65·4 ± 2·12 (7)
H45 *clio*		89·7 ± 2·49 (6)	85, 86	66, 66·5, 68·5, 69·5 (2)	66·5
H47a *collaris*		94, 96·5*	92	65·5, 68·5*	63
	M	94·7 ± 2·16 (6)	—	65 (2), 67, 68, 70	—
H47b *misimae*		93, 94	90·5, 92	64·5, 65	63, 65·5
	M	93·3 ± 1·98 (7)	—	65·6 ± 1·62 (7)	—
H47c *rosseliana*		96·5	90	66·5	—
	M	95·0 ± 1·26 (6)	—	65·8 ± 0·98 (6)	—
H48a *citreogaster*		92	87	64·5	65·5
H48b ,,		85·1 ± 1·85 (7)	8·15, 83·5	60·9 ± 2·07 (7)	57, 59·5
H48c ,,		87·5, 90	84·5	62	62·5
H48d *sexuvaria*		85	87	59	62·5
H49 *ottomeyeri*		104	—	73·5	—
H50 *tabarensis*	M	99·1 ± 1·88 (7)	91, 94	70·1 ± 0·99 (7)	67, 68·5
H51 *goodsoni*		91·5	88	65	61·5
H52a *ornata*		98*	—	69*	—
	M	95·7 ± 1·16 (10)	91·6 ± 1·76 (13)	66·8 ± 1·56 (9)	64·0 ± 1·71 (12)
H52b ,,	M	95·0 ± 5·15 (41)	90·2 ± 1·91 (25)	64·5 ± 2·33 (42)	62·4 ± 1·83 (23)
H53 *utupuae*		88·5, 91, 93*	88*	62, 63·5, 65·5*	63·5*
	M	92·4 ± 1·26 (13)	89·1 ± 0·83 (11)	64·5 ± 1·37 (11)	62·1 ± 1·45 (10)
H54 *kandavensis*		90 (2), 92	85·5, 91	60, 65, 67·5	61, 62, 63
	M	89·4 ± 2·37 (16)	87·0 ± 1·04 (11)	66·1 ± 1·18 (15)	64·5 ± 0·93 (11)
H55 *vitiensis*		90*, 90·5	—	60·5, 62·5*	—
	M	91·1 ± 1·45 (9)	88·1 ± 1·17 (9)	61·6 ± 1·94 (9)	59·3 ± 0·95 (7)
H56 *lauana*		97*	—	69*	—
	M	96·7 ± 1·93 (21)	93·2 ± 1·52 (16)	66·3 ± 2·32 (20)	64·7 ± 1·54 (15)
H57 *melanops*		101·8 ± 2·22 (8)	95	70·1 ± 2·28 (8)	67·5
	M	103·6 ± 1·26 (19)	97·0 ± 1·28 (12)	70·7 ± 1·48 (19)	67·7 ± 0·49 (12)
P. flavifrons		86·0 ± 2·15 (14)	81·5, 83·5, 84·5, 86	58·1 ± 1·82 (12)	56, 57, 58, 61
	M	87·5 ± 1·53 (20)	83·6 ± 1·09 (18)	59·4 ± 2·22 (19)	56·8 ± 1·58 (20)

	Tarsus	Culmen	Bill depth
P. schlegelii			
1 *schlegelii*	23 (2)	—	5, 6
2 *cyclopum*	23·5 (2)	17 (2)	5·5
3a *viridipectus*	23·9 ± 0·79 (18)	15·6 ± 0·59 (17)	5·4 ± 0·38 (17)
3b *obscurior*	23·9 ± 0·65 (20)	16·0 ± 0·46 (20)	5·3 ± 0·15 (15)
P. soror			
1 *soror*	22·4 ± 0·38 (6)	16·5, 17	5·7 ± 0·42 (6)
2 *klossi*	22·1 ± 0·56 (20)	17·2 ± 0·38 (13)	5·9 ± 0·49 (17)
3 *bartoni*	22·2 ± 0·68 (22)	17·1 ± 0·61 (21)	5·5 ± 0·46 (21)
P. pectoralis			
A1 *fulviventris*	21·7 ± 0·87 (9)	18·7 ± 0·87 (9)	6·5 ± 0·53 (8,
A2a *javana*	19, 20, 20·5	16·5, 17, 18	5·5, 6
A3a *fulvotincta*	20·5 ± 0·96 (12)	18·0 ± 0·80 (12)	6·4 ± 0·48 (7)
A3b *jubilarii*	20·5, 21, 21·5 (2), 22·5	18 (3), 18·5, 19	5·5, 6 (3), 6·5
A4 *everetti*	22·4 ± 1·02 (6)	20·4 ± 0·74 (6)	6 (2), 6·5, 7 (2)
A5 *teysmanni*	21, 22	18, 19	5·5, 6
B6 *mentalis*	21·8 ± 0·67 (15)	19·4 ± 0·82 (15)	6·5 ± 0·56 (9)
B7 *tidorensis*	23·5 ± 0·55 (6)	20·9 ± 0·38 (7)	7·3 ± 0·24 (6)
	23·5 (2), 24 (3)[1]	21·2 ± 0·42 (6)[1]	7·1 ± 0·38 (6)[1]
B8 *obiensis*	23·0 ± 0·64 (7)	22·1 ± 0·56 (7)	6·9 ± 0·30 (7)
C9 *bougainvillei*	25 (2), 25·5, 26	22·5 (2), 23, 23·5	7, 7·5, 8, 8·5
M	—	23·0 ± 0·95 (6)	—
C10a *orioloides*	23, 25 (2)	22, 23	7·5, 8·5 (2)
C10b ,,	25	24·5	9
C10c *pavuvu*	24·5, 26·5	23, 24	8, 9
C11 *cinnamomea*	24·7 ± 0·88 (37)	22·7 ± 0·87 (35)	8·1 ± 0·38 (33)
C12 *sanfordi*	25, 26	22, 23	8 (2)
C13a *melanonota*	24·5 (2)	25	8, 8·5
C14 *melanoptera*	24·5, 26	23 (2)	7
C15 *centralis*	24·5 (2)	24, 24·5	8, 8·5
C16 *feminina*	26·5 ± 0·98 (7)	22·7 ± 0·87 (7)	6·7 ± 0·26 (6)

[1] Wrongly or inadequately localized specimens, separated from *mentalis* (type (♂): tarsus 21·5, culmen 19·5, bill depth 7) on measurements.

	Tarsus	Culmen	Bill depth
C17a *christophori*	24·8 ± 0·78 (93)	20·8 ± 0·67 (82)	6·8 ± 0·39 (70)
,, ♂ ad.	24·7 ± 0·85 (44)	20·9 ± 0·63 (39)	6·8 ± 0·30 (35)
,, ♀ ad.	25·1 ± 0·58 (20)	20·8 ± 0·52 (18)	6·8 ± 0·47 (14)
,, ♂ II phase	25·0 ± 0·72 (10)	20·7 ± 0·56 (9)	6·6 ± 0·42 (8)
,, ♂/♀ I phase	24·7 ± 0·77 (15)	20·8 ± 1·04 (13)	6·8 ± 0·52 (11)
D18a *graeffii*	26, 27 (2), 27·5 (2)	18·5, 19, 20 (3)	6, 6·5 (2), 7
D18b *optata*	26·5 ± 0·50 (9)	19·0 ± 0·61 (9)	6·4 ± 0·32 (8)
D19a *aurantiiventris*	23, 24·5, 25 (2), 26	18, 18·5, 19 (2), 20	6·5 (3), 7 (2)
D19c *ambigua*	24·5, 25·5 (2)	18, 19·5 (2)	7
D20a *torquata*	27·0 ± 0·78 (16)	19·3 ± 0·85 (15)	6·4 ± 0·49 (13)
D20b *koroana*	25·5, 27	19, 20	6.5
E22a *bynoei*	24	20	5
E22b *melanura*	23, 23·5 (2)	18·5 (3)	5·5, 6, 6·5
E22c ,,	22·5 (2), 23 (3)	18 (5)	5 (2), 5·5 (2), 6
E22d *hilli*	22, 23·5	18, 18·5	5·5
E23 *violetae*	21·5, 22·5, 23·5, 24	18, 19 (3), 19·5	6 (4)
E24 *spinicauda*	23·0 ± 0·81 (12)	19·6 ± 0·75 (10)	5·9 ± 0·54 (11)
E25a cf. *dahli*	23·5	—	—
E25b "*innominata*"	24·5 (2)	20, 20·5	6, 6·5
E25c *fergussonis*	24·5	19·5	6·5
E25d *dahli*	23·5, 24	19, 19·5	6·5 (2)
E25e ,,	22·5, 23, 24	18·5, 20	5·5, 6·5, 7·5
E25g ,,	23·7 ± 0·97 (9)	19·6 ± 0·32 (8)	6·0 ± 0·25 (9)
E25j ,,	22·5 (2)	20·5 (2)	6·5, 7·5
E25k ,,	23·5, 24·5	19·5, 21	6·5 (2)
E26 *whitneyi*	24·7 ± 1·75 (6)	(19·5, 20·5, 21, 21·5, 22)*	6·5 (2), 7·5
M	—	20·1 ± 1·06 (15)	—
E27 *balim*	24, 25	18·5 (2)	6, 7
F28a *occidentalis*	22·4 ± 0·78 (24)	16·6 ± 0·71 (22)	5·3 ± 0·32 (24)
F28b *fuliginosa*	21·7 ± 0·68 (6)	16·3 ± 0·82 (6)	5, 5·5 (2), 6 (2)
F29 *glaucura*	22·9 ± 0·69 (8)	15·7 ± 0·91 (9)	5·7 ± 0·57 (9)
F30a *youngi*	21·9 ± 0·79 (8)	16·9 ± 0·48 (7)	5·4 ± 0·32 (8)
F30b *pectoralis*	21·6 ± 0·61 (10)	17·2 ± 0·85 (8)	5·4± 0·35 (8)
F31a *ashbyi*	22·3 ± 1·49 (8)	17·2 ± 1·60 (8)	5·6 ± 0·45 (7)
F31b *queenslandica*	21·7 ± 0·98 (6)	17·2 ± 0·61 (6)	5·7 ± 0·41 (6)
F32 *contempta*	22·5 ± 0·68 (14)	18·6 ± 0·59 (14)	5·8 ± 0·45 (12)

	Tarsus	Culmen	Bill depth
F33 *xanthoprocta*	25·4 ± 0·54 (20)	19·5 ± 0·46 (20)	6·3 ± 0·38 (19)
G34 *caledonica*	24·2 ± 1·17 (11)	18·5 ± 0·76 (11)	5·1 ± 0·46 (10)
G35 *littayei*	26 (2), 27 (2), 28·5	23, 24, 24·5 (3)	7·5 (2), 8 (2), 8·5
G36 *cucullata*	25·6 ± 0·49 (6)	19·7 ± 0·27 (6)	5·6 ± 0·38 (6)
G37a *chlorura*	24·5, 25·5	19, 19·5 (2)	6 (2), 7
G37b *efatensis*	24·7 ± 0·98 (6)	19·2 ± 0·61 (6)	6·1 ± 0·38 (6)
G37c *brunneipectus*	24·5	20	6
G37d *intacta*	24·5 ± 0·69 (13)	19·5 ± 0·78 (13)	6·2 ± 0·32 (13)
G37e cf. *banksiana*	25	20	—
G37f *banksiana*	25, 26	20	7
G38 *vanikorensis*	23·5, 24·5 (2), 25·5	19, 19·5 (2), 20	5, 6 (2)
H39a *calliope*	24·0 ± 0·87 (9)	21·0 ± 0·61 (9)	6·9 ± 0·52 (8)
H39b *arthuri*	23·5, 24	22·5 (2)	7, 7·5
H40 *sharpei*	25, 25·5, 26	21, 22, 23	7 (2), 7·5
H41 *dammeriana*	25 (2)	22·5, 23	7, 8
H42 *fuscoflava*	26, 28, 28·5, 29·5	24 (2), 24·5, 26	8·5 (2)
H43a *alfurorum*	22·9 ± 0·83 (8)	19·9 ± 0·64 (8)	6·6 ± 0·34 (7)
H43b *macrorhyncha*	22·7 ± 1·14 (19)	20·1 ± 0·75 (18)	6·5 ± 0·50 (17)
H44 *buruensis*	23·4 ± 0·81 (25)	19·1 ± 0·55 (25)	6·1 ± 0·31 (23)
H45 *clio*	22·3 ± 0·22 (11)	19·4 ± 1·03 (9)	6·6 ± 0·44 (11)
H47a *collaris*	24·5 (2), 25	22·5, 23	6·5 (2), 7·5
H47b *misimae*	23·5, 24·5, 25, 25·5	23 (2), 23·5, 24	6, 6·5, 7·5
H47c *rosseliana*	24·5, 25	23, 25	6·5
H48a *citreogaster*	22·5, 23	18·5, 19	6·5, 7
H48b ,,	22·3 ± 0·62 (9)	19·0 ± 0·71 (8)	6·2 ± 0·61 (9)
H48c ,,	20·5, 22·5, 23	18·5, 19, 20	6, 6·5, 7
H48d *sexuvaria*	24, 24·5	19·5, 20	6·5 (2)
H49 *ottomeyeri*	25·5 (2)	22·5, 24	7, 7·5
H51 *goodsoni*	22, 23	20·5 (2)	6·5, 7·5
H52a *ornata*	26, 26·5	21	7·5 (2)
H53 *utupuae*	25, 25·5, 26·5 (2)	20, 20·5, 21 (2)	6, 6·5, 7, 7·5
H54 *kandavensis*	25·9 ± 1·02 (8)	18·4 ± 0·86 (8)	6·3 ± 0·46 (8)
H55 *vitiensis*	24, 25·5	18·5, 19	6, 7
H56 *lauana*	25, 26	20	6·5
H57 *melanops*	26·4 ± 0·85 (11)	20·7 ± 0·67 (9)	7·0 ± 0·50 (11)
P. flavifrons	24·5 ± 0·71 (26)	18·8 ± 0·78 (27)	6·1 ± 0·42 (24)

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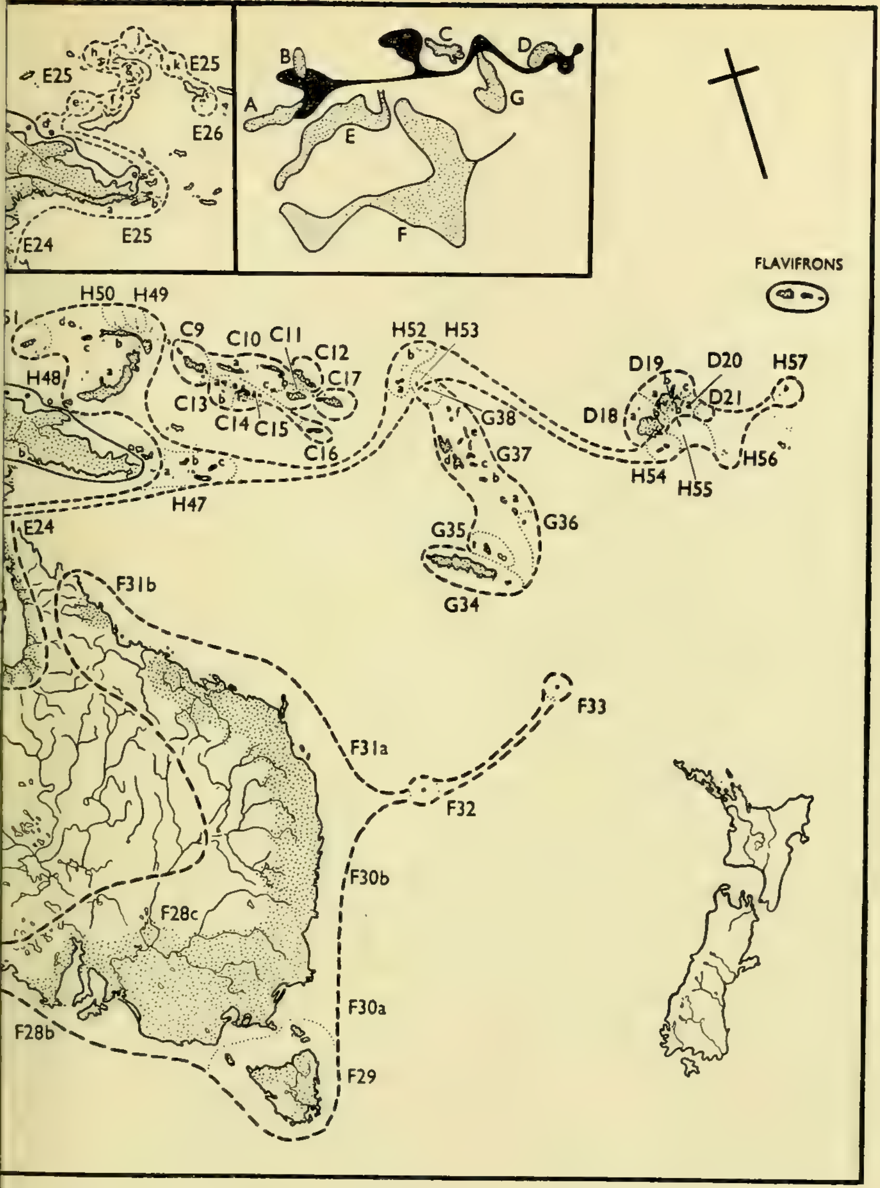
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F28c
F30a
F28b
F29

cies. Solid lines, boundaries of *P. schlegelii*, *P. soror* and *P. flavifrons*; broken lines,
lotted lines, boundaries of subspecies (omitted where continental subspecies intergrade).
E of *P. pectoralis* in the Papuan region. Inset right, relative positions of the subspecies-
ead group H black.

rn San Cristobal C17a: the corresponding suffixes have been omitted from the map).

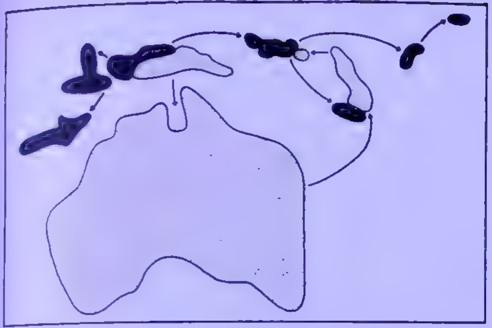


Fig. 7. Diagram (for comparison with Fig. 6) showing original colonizations by the [illegible] emblage (black) and the *soror* assemblage (stippled). Group H of *P.* [illegible] mitted (see Fig. 6, inset right)

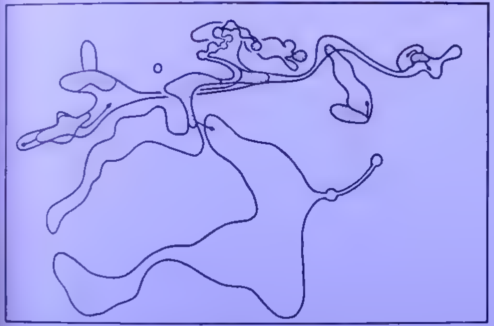
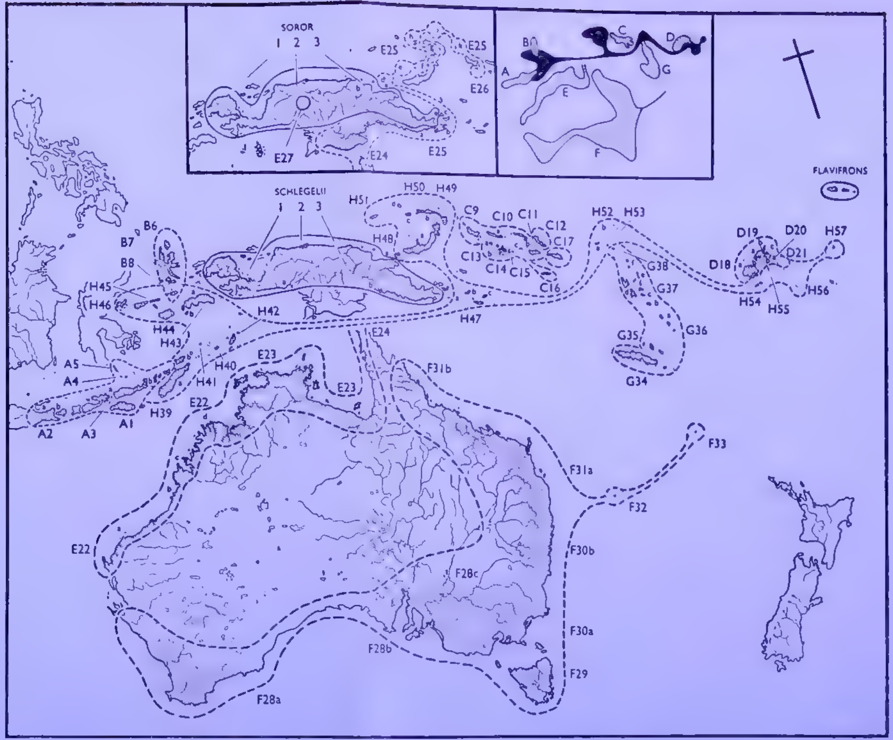


Fig. 8. Diagram (for comparison with Fig. 6) showing areas of secondary intergradation between subspecies-groups of *P. pectoralis* (stippled), and minor gene-flow (arrows).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C14 C15
C16
C17
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B6
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F33
F32
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F28c
F30a
F28b
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F28a

Fig. 6. Sketch-map of the distribution of the superspecies. Solid lines, boundaries of *P. schlegelii*, *P. soror* and *P. flavifrons*; broken lines, boundaries of the subspecies-groups of *P. pectoralis*; dotted lines, boundaries of subspecies (omitted where continental subspecies intergrade). Inset left, distribution of *P. soror* and subspecies-group E of *P. pectoralis* in the Papuan region. Inset right, relative positions of the subspecies-groups of *P. pectoralis*: groups A to G stippled, widespread group H black.

(Santa Anna C17b lies off south-eastern San Cristobal C17a: the corresponding suffixes have been omitted from the map).

A REVISION OF THE LAKE VICTORIA *HAPLOCHROMIS* SPECIES (PISCES, CICHLIDAE)

PART I: *H. OBLIQUIDENS* HILGEND., *H. NIGRICANS* (BLGR.), *H. NUCHISQUAMULATUS* (HILGEND.) AND *H. LIVIDUS*, SP. N.

P. H. GREENWOOD

PRESENTED

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BY

P. H. GREENWOOD

East African Fisheries Research Organization, Jinja, Uganda.

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INTRODUCTION

The species described in this paper form a well-defined ecological group within the *Haplochromis* species flock of Lake Victoria. All feed principally by grazing on epiphytic and epilithic algae.

As a group and severally they show obvious morphological adaptations to this particular feeding habit. Adaptation is most clearly seen in tooth-form and arrangement, which depart from those common to the majority of *Haplochromis* species.

Several other ecologico-morphological groups have evolved in Lake Victoria. Their existence raises questions regarding the possibility of providing a realistic basis for subdividing the present phylogenetically amorphous arrangement of the species.

There are, however, certain difficulties inherent in this procedure. A strictly morphological approach to sub-division is unworkable. Intergradation, rather than discreteness, of morphological group-characters might be said to typify this species flock. Such a situation is, however, not unexpected in a large group of oligophyletic origin which has undergone intense adaptive radiation during a short period of geological time (Regan, 1922 ; Greenwood, 1951).

Also, although some morphologically distinct species-complexes occupy equally distinctive ecological niches, there are other morphologically-homogeneous groups which cut across any attempted ecological classification.

Furthermore, in any ecologically-defined group there are grades of anatomical specialization such that the most and least specialized species are only with difficulty included in a supra-specific category defined by morphological criteria alone. The species described here typify this situation. Tooth-form in *H. obliquidens* is unlike that of most species at present included in the genus *Haplochromis*. Yet three algal-grazing species are known, which partially bridge this morphological gap. At the opposite extreme *H. nuchisquamulatus* exhibits incipient dental adaptation only slightly removed from a generalized *Haplochromis* type.

In Lake Victoria, then, there exist several nascent supra-specific groups which are more readily identified by ecological than morphological criteria. Since conventional taxonomic characters are, so to speak, also nascent, formal recognition of these categories is impossible. I propose, therefore, to recognize their biological and evolutionary significance only by drawing attention to their existence.

Haplochromis obliquidens Hilgendorf, 1888

Chromis (*Haplochromis*) *obliquidens* Hilgendorf, 1888, *S. B. Ges. naturf. Fr. Berlin*, 76.
Ctenochromis obliquidens, Pfeffer, 1897, *Arch. f. Naturg.*, **63**, 60.
Tilapia obliquidens, Boulenger, 1898, *Trans. zool. Soc., Lond.*, **15**, 5.
Hemitilapia bayoni Boulenger, 1908, *Ann. Mus. Genova* (3) **4**, 6 ; *Idem*, 1911, *Ibid.* (3) **5**, 69 ; *Idem*, 1915, *Cat. Afr. Fish.*, **3**, 491, fig. 340.
Haplochromis nuchisquamulatus (part), Boulenger, 1915, *op. cit.*, 290.
Clinodon bayoni (Blgr.), Regan, 1920, *Ann. Mag. nat. Hist.* (9), **5**, 33.
Haplochromis obliquidens (part), Regan, 1922, *Proc. zool. Soc., Lond.* 188.

The holotype of *Haplochromis obliquidens* could not be examined; it is amongst those specimens, once housed in the Berlin Museum, and which cannot be located at present. However, the characters noted in Hilgendorf's original description are diagnostic.

Through the courtesy of Dr. D. Guiglia (Museo Civico di Storia Naturale, Genoa) I was able to study the holotype of *Hemitilapia bayoni* Boulenger, and thus to confirm Regan's synonymy of this species with *H. obliquidens*.

On the other hand, I cannot agree with Regan's tentative synonomy of *Hemitilapia materfamilias* Pellegrin, 1913, and *Haplochromis obliquidens* (Regan, 1922). Re-examination of *H. materfamilias* type specimen revealed that Pellegrin's original description is misleading, particularly in respect of the dentition, and that the species should be referred to *Macropleurodus bicolor* (Blgr.) (Greenwood 1956).

Description. Based on fifty-seven fishes (size range 48–89 mm. standard length) including the holotype of *Hemitilapia bayoni* and five specimens in the British Museum (Natural History). Three other British Museum (Nat. Hist.) specimens were examined, but are not included in the morphometric data.

Since no marked allometry with size was determined for any character examined, measurements are given for the collection as a whole, with the exception of the smallest specimen, which is treated separately.

Depth of body 33·4–41·2, mean (M) 37·5, length of head 29·4–34·0 (M = 32·3) per cent of standard length. Dorsal profile of head and snout straight; fairly steeply sloping in most fishes but decurved in a few individuals. Preorbital depth 12·5–17·4 (M = 15·2) per cent of head length; least interorbital width 27·8–34·7 (M = 31·8); snout as broad as or somewhat broader than long, rarely longer than broad, its length 26·6–33·3 (M = 29·2) per cent head length. Eye 29·1–33·3 (M = 31·4); depth of cheek 19·0–25·0 (M= 21·5) per cent head length.

Caudal peduncle about 1½ times as long as deep; 13·2–16·4 (M = 15·0) per cent of standard length.

Corresponding ratios for the smallest individual (48 mm. S. L.)—not included in the mean values given above—are: Head 32·3; preorbital 11·1; interorbital 27·8; snout 27·8; eye 27·8; cheek 16·7; and caudal peduncle 16·6 per cent.

Mouth short and horizontal or very slightly oblique; posterior maxillary tip extending to the vertical from the anterior orbital margin, or almost so. Jaws equal anteriorly, the lower 31·6–41·6 (M = 37·2) per cent of head length; its length/breadth ratio from 1·1–1·7 (mode 1·4).

Gill rakers short; 8 or 9, rarely 7 or 10, on the lower limb of the anterior arch.

Scales ctenoid; lateral line interrupted, with 30 (f.6), 31 (f.31) or 32 (f.18) scales. Cheek with 3 (rarely 2 or 4) series of imbricating scales. 5 or 6 scales between the dorsal fin origin and the lateral line; 5–7 between pectoral and pelvic fin insertions.

Fins. Dorsal with 24 (f.25), 25 (f. 31) or 26 (f.1) rays, anal 10 (f.1), 11 (f.11), 12 (f.43) or 13 (f.2), comprising XIV–XVI, 8–10 and III, 7–10 spines and soft rays for the fins respectively. First pelvic ray slightly produced and variable in its posterior extension, usually reaching the spinous anal fin in adults and occasionally to the soft part in ripe males. Caudal sub-truncate.

Teeth. Teeth forming the outer series are movably implanted and have slender necks with undivided, expanded, compressed and obliquely truncate crowns (Text-fig. 1). In many specimens a few postero-lateral teeth in both jaws are bicuspid but otherwise retain almost the same crown form as the more anterior teeth ; in some the second cusp is incipient, but in others it is clearly differentiated. There is no correlation between length of fish and the presence or number of undifferentiated postero-lateral teeth.

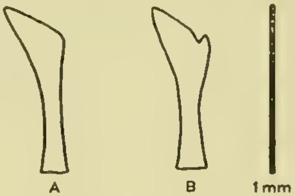

Fig 1.

A weak positive correlation exists between the number of teeth in the outer series of the upper jaw, and standard length.

S.L. (mm.)	48	55–64	65–74	75–87
Tooth number	50	42–60	50–70	58–70
Mean	50	54	59	64
N	1	20	21	12

The inner teeth are mostly tricuspid and arranged in 2–4 rows, with a distinct interspace separating them from the outer series. Some obtusely tricuspid teeth, and others differing only in their smaller size from those in the outer series, frequently occur in the first inner row. These obliquely truncate teeth are larger than their tricuspid associates.

Alizarin preparations of two larvae (10 and 11 mm. total length) obtained from the mouth of a brooding female, show larval dentition to be comparable with that of *H. macrops* (Blgr.) *H. prodromus* Trewavas and *Macropleurodus bicolor* at an equivalent developmental stage. The teeth of *H. obliquidens* larvae differ considerably from the adult condition, being slender and setiform, with slightly recurved unicuspid crowns ; 14–16 outer teeth, aggregated medially, are present in the upper jaw.

In certain fishes from Kisumu, it was noticed that the crowns of all teeth were coarse and irregular, and that their typical golden-brown coloration was replaced by black. Similar structural differences and discoloration have been observed in specimens of *H. michaeli* Trewavas from various localities. The cause of this aberrancy is unknown.

Lower pharyngeal bone sub-equilaterally triangular, its dentigerous surface broader than long. The numerous teeth are fine, compressed and directed posteriorly, and have truncated crowns ; a small anterior cusp is present in all.

Skeleton. Differs in no important respect from that of generalized *Haplochromis* species. Vertebrae: 14 + 17, 13 + 17, 13 + 16 or 12 + 17.

Coloration in life: Breeding males. Ground colour bright yellow-green, becoming yellower ventrally; chest and branchiostegal membrane blackish; lips slightly irridescent. Dorsal fin yellow-grey, lappets red; orange-red spots and streaks on the posterior spinous and entire soft parts. Anal with a pinkish flush; 3 or 4 yellow ocelli. Pelvics with black outer and clear or faint pink inner half. Non-breeding adult males are similarly coloured except that the body is more nearly olivaceous and the chest not darkened. *Females and juveniles of both sexes.* Ground colour silvery-yellow. Dorsal and caudal fins neutral; anal and pelvic fins pale yellow. Darker, almost olivaceous females are known.

Transverse banding occurs in both sexes, but is rarely apparent in life.

Preserved material: Adult males. Dusky, the vertical bars partly or completely obscured. Dorsal fin sooty, lappets black, the posterior spinous and entire soft part maculate; anal colourless; pelvics dark laterally, pale mesially; caudal maculate. *Females and juveniles.* Grey to brown, with or without six to ten narrow transverse bars on the flanks; less frequently a faint mid-lateral stripe and a fainter stripe approximately following the upper lateral line. Fins colourless and immaculate.

Distribution. Haplochromis obliquidens has been collected from many localities in Lake Victoria. It is also known from the Victoria Nile.

Recently, Miss R. H. Lowe obtained a small sample of *H. obliquidens* from Lake Bunyoni (Uganda). Earlier reports (Worthington, 1932) indicated the probability that no *Haplochromis* were then present in this lake. It is presumed that those now occurring there were accidentally introduced on occasions when the lake has been stocked with *Tilapia* species; that one of the two species now recorded is probably *H. nigripinnis* Regan (otherwise endemic to Lake Edward) and the other is *H. obliquidens* supports this assumption, since *Tilapia* have been introduced from both Lakes Edward and Victoria.

The nine Lake Bunyoni *H. obliquidens* (size range 63–85 mm. S.L.) differ slightly from the Lake Victoria population in the following characters: body more slender, 30·2–34·5 (M = 32·4) per cent of standard length; the preserved coloration of sexually mature males is apparently more melanic; in three specimens the outer series of teeth is entirely composed of bicuspids similar to the undifferentiated postero-lateral teeth of Lake Victoria fishes. In all other observed morphological characters the two populations are identical.

Ecology: Habitat. Shallow littoral zone, particularly in the vicinity of emergent vegetation; less commonly in the water-lily zone, over exposed sandy beaches and at the margin of papyrus swamps. There are indications, both from fishing and direct observation, that *H. obliquidens* may frequent rocky shore-lines, where the substrate is largely composed of broken rocks and boulders. The species has often been collected and seen around rock foundations of piers.

Food. The intestine of *H. obliquidens* is long and much coiled ($2\frac{1}{2}$–3 times S.L.); stomach large and distensible. Stomach and intestinal contents of fifty-three individuals (size range 48–89 mm. S.L.) from various localities, have been examined.

Diatoms comprised the main digested contents in forty-four individuals; the genera principally recorded were: *Melosira*, *Suririella*, *Gomphonema*, *Rhopalodia*, *Navicula* and *Cyclotella*.

Small fragments of plant epidermis occurred in the stomachs of twenty-nine fishes. The quantity ingested by individuals varied considerably. It was observed that, unless ruptured, most epidermal cells were apparently undigested.

Blue-green algae, especially *Rivularia* and *Microcystis*, and less frequently *Anabaena* and *Oscillatoria*, were recorded from nineteen stomachs; none of these plants showed signs of digestion.

Filamentous green algae, chiefly *Spirogyra* and to a lesser extent *Oedogonium*, occurred in sixteen stomachs. No digestion was noted.

The stomach contents of one individual comprised only partly digested fragments of Ephemeroptera larvae, probably taken at the time of their emergence. Fragmentary remains of both adult and larval insects were found in the intestines of three other fishes.

The frequent occurrence of epiphytic algae and epidermal fragments of phanerogams suggests that *H. obliquidens* feeds partly by scraping the surface of submerged leaves and stems. This supposition is confirmed by observations made on the feeding behaviour of these fishes in the lake; the peculiar dentition of *H. obliquidens* would seem to be highly adapted for such habits.

On the other hand, sand grains and bottom debris were also found in many stomachs; indeed, it was often difficult to determine whether ingested plant fragments were the partly digested remains of epidermis scraped from living plants or whether they were derived from the semi-decayed debris which accumulates near dense plant stands. Probably *H. obliquidens* feeds both by grazing on plants and by utilizing plant material contained in the bottom detritus. In either eventuality it is clear that diatoms are the principal food organisms utilized, and that much ingested plant material is voided undigested.

Although rather infrequent, the occurrence of insects in the pabulum could indicate that the species is partly facultative in its feeding habits and may utilize temporary and seasonal abundances of animal food.

Breeding. Breeding behaviour and spawning sites of *H. obliquidens* are unknown. However, females carrying young in the buccal cavity have been obtained from most localities.

The smallest sexually active fish was a female 61 mm. long; above 68 mm. S.L., most individuals were found to be mature.

Affinities and taxonomic status of the species

Particular interest attaches to *H. obliquidens*, since although it is the type species of the genus its dental morphology is unique amongst the very numerous species of *Haplochromis*. Throughout this discussion the generic diagnosis is taken to be that prepared by Regan (1920) in which particular emphasis was laid on neurocranial osteology. Subsequently this definition has been modified by the recognition of several related genera distinguished from *Haplochromis* by their divergent dentition (Regan, 1922; Trewavas, 1938; Greenwood, 1956).

Within the genus thus defined two types of outer teeth predominate, a unicuspid, conical form and a bicuspid compressed type. The common dental pattern is a single outer series distinctly separated from the inner series, usually comprising two or three rows anteriorly and a single row postero-laterally.

Tooth form and pattern have played an important part in species discrimination and in the actual or attempted delimitation of supra-specific groups amongst Lake Victoria species. Extreme dental specialization, associated with osteological changes, characterises four of the five monotypic cichlid genera in this lake (Regan, 1922; Greenwood, 1956), whilst less obvious dental characters were used in an attempt to subdivide the endemic *Haplochromis* into five genera (Regan, 1920). Two years later, Regan abandoned this concept, reducing some of his genera to subgeneric rank and discarding others (*idem*, 1922).

Because the dental morphology of *H. obliquidens* does not conform with that usual for *Haplochromis*, there might appear to be grounds, as Regan suggested (*op. cit.*), for recognizing at least one sub-genus to accommodate those species with unequally bicuspid or conical outer teeth. The sub-genus *Ctenochromis* (Pfeffer, 1893) would be available for such species (Regan, *loc. cit.*). In that paper Regan first indicated *H. astatodon* Regan of Lake Kivu as providing a dental type, which although invariably bicuspid, linked the " *obliquidens* " tooth form with that of the commonly occurring *Ctenochromis* type. The teeth of *H. astatodon* exhibit some diversity in the degree to which they approach the " *obliquidens* " condition, but the greatest number of individuals has teeth approximating more closely to this type than to " *Ctenochromis* ". The common tooth form in *H. astatodon* may be likened to a bicuspid variant of typical *H. obliquidens* teeth; indeed, similar teeth frequently occur postero-laterally in both jaws of *H. obliquidens*.

Two other annectent species have since been found: *H. annectidens* Trewavas from Lake Nabugabo and a new species (described below) from Lake Victoria. Intra-specific variation in the tooth form of this latter species is as great as that of *H. astatodon*, but most individuals possess teeth similar to the undifferentiated postero-lateral teeth of *H. obliquidens*.

It is clear, then, that although the teeth of *H. obliquidens* may represent an extreme form, intermediates linking them to the usual bicuspid *Haplochromis* type are found as the characteristic dentition in three extant species. The gap separating the most " *obliquidens* "-like teeth of *H. astatodon* and the new species from those of *H. obliquidens* is relatively slight; it represents no more than the loss of a small cusp from an expansive, compressed and obliquely truncate crown. Less modified crown structure as seen in some teeth of these two species, grades through the condition found in *H. nuchisquamulatus*, into the more usual, acutely bicuspid form.

Thus, the case for recognizing at least two sub-genera of *Haplochromis* on the basis of dental morphology (Regan, 1920 and 1922) is weakened. As was mentioned earlier, several ecologically defined groups, each comprising apparently related species, are known from Lake Victoria. In every case, the group shows certain morphological divergence from the generalized *Haplochromis* type, but no clear-cut gap has evolved which would allow for its formal recognition as a sub-genus.

Study material and distribution records

Museum and Reg. No.	Locality.	Collector.
Genoa Museum. Holotype of *Hemitilapia bayoni*	Sesse Islands	Bayon.
British Museum (N.H.) 1908, 10.19.6 (paratype of *H. bayoni*)	Sesse Islands	Bayon.
British Museum (N.H.) 1911, 3.3.80	Jinja (Ripon Falls)	Bayon.
British Museum (N.H.) 1913, 9.30.13–18	Lake Victoria	Bayon.
British Museum (N.H.) 1956, 7.9.1–16	Jinja (Pier)	E.A.F.R.O.
,, ,, ,, ,, ,, ,, 17–20	Beach near Nasu Point (Buvuma Channel)	,,
,, ,, ,, ,, ,, ,, 21–27	Grant Bay (Buvuma Channel)	,,
,, ,, ,, ,, ,, ,, 28	Napoleon Gulf, near Bugungu (opp. Jinja)	,,
,, ,, ,, ,, ,, ,, 29–32	Entebbe Harbour	,,
,, ,, ,, ,, ,, ,, 33–45	Kisumu, Kavirondo Gulf	,,
,, ,, ,, ,, ,, ,, 46–55	Mwanza, Capri Bay	,,
,, ,, ,, ,, ,, ,, 56–57	Godziba Island	,,
,, ,, ,, ,, ,, ,, 169–170	Kalagala, Victoria Nile	,,

Haplochromis lividus sp. nov.

Haplochromis nuchisquamulatus (part), Blgr., 1915, *Cat. Afr. Fish.*, **3**, 290, Fig. 197.
Haplochromis desfontainesii (part), Blgr., 1915, *op. cit.*, 302.
Haplochromis nubilus (part), Regan, 1922, *Proc. zool. Soc., London*, 164.

Type specimen. A male 90 + 21 mm. from Bugungu (near Jinja), Uganda.

Description. Based on seventy-seven fishes (size range 46–90 mm. S.L.) from Lake Victoria. Five specimens from Lake Kyoga are considered separately.

Within the size range of individuals studied no character showed marked allometry with standard length or length of head; measurements are therefore given for the whole collection with the exception of the smallest fish, which was not included when determining means.

Depth of body 33·3–41·2 (M = 36·5); length of head 31·0–35·0 (M = 32·7) per cent of standard length. Dorsal head profile straight and moderately steeply sloping (*ca.* 45°), rarely somewhat curved. Preorbital depth 12·0–16·7 (M = 14·7) per cent head length; least interorbital width 26·2–33·3 (M = 29·7); snout as broad as long, its length 26·0–32·0 (M = 28·8) per cent of head. Eye 28·0–36·0 (M = 31·4); depth of cheek 17·0–24·1 (M = 20·1) per cent head length.

Caudal peduncle 1·1–1·7 (M = 1·4) times as long as deep; 12·2–18·5 (M = 15·5) per cent standard length.

Corresponding ratios for the smallest fish (46 mm. S.L.) are: Depth 39·0, head 39·0 per cent of standard length. Preorbital 12·8, interorbital 23·2, snout 27·8 and cheek 16·7 per cent of head-length. Caudal peduncle 15·2 per cent of S.L.

Mouth horizontal or slightly oblique; posterior maxillary tip reaching the vertical to the anterior orbital margin or nearly so, and to the eye in some. Lips slightly thickened. Lower jaw 33·3–41·0 (M = 37·2) per cent of head, its length/breadth ratio 1·3–2·0 (mode 1·6).

Gill rakers short, 8 or 9 (less frequently 7 or 10) on the lower part of the first arch.

Scales ctenoid, lateral-line interrupted, with 30 (f.7), 31 (f.16), 32 (f.48), 33 (f.5), or 34 (f.1) scales. Cheek with 2 or 3 (rarely 4) series. 5 or 6 scales between dorsal fin origin and the lateral line ; 5 or 6 between pectoral and pelvic fin insertions.

Fins. Dorsal with 23 (f.1), 24 (f.34), 25 (f.40) or 26 (f.2) ; anal 11 (f.18), 12 (f.55), and 13 (f.4), rays, comprising XV–XVI 8–10 and III, 8–10 spinous and soft rays for the fins respectively. First pelvic ray produced, variable in its posterior extension, but reaching the spinous anal in most adults. Pectoral fins as long as, or slightly shorter than the head. Caudal sub-truncate.

Teeth. In the form and pattern of its teeth, *H. lividus* departs from the generality of *Haplochromis* species. The anterior and antero-lateral teeth in the outer series are movably implanted and have slender necks (somewhat stouter than in *H. obliquidens*) with compressed, expanded and obliquely truncated, unequally bicuspid crowns. The posterior cusp shows some variation in size, but it is always smaller than the anterior, from which it is narrowly separated (Text-fig. 2). It should be noted that these teeth bear a striking resemblance to the undifferentiated posterolateral teeth of *H. obliquidens*. Posterolateral teeth in *H. lividus* are either similar to the anterior teeth or indistinguishable from the generalized acutely bicuspid type (Text-fig. 2G). Less frequently, unicuspid teeth occur in this position. A weak positive correlation exists between the number of teeth in the outer series of the upper jaw and standard length.

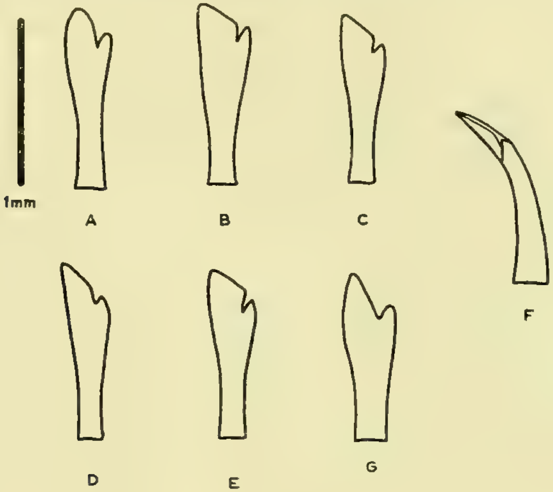

FIG. 2

S.L. (mm.)	46	56–65	66–75	76–85	86–91
Tooth number	36	42–58	38–66	44–75	52–66
Mean	36	50	54	61	57
N	1	8	27	33	5

Teeth forming the inner rows are invariably tricuspid and small. No obtusely cuspidate teeth, or teeth similar to those of the outer series, have been observed (*cf. H. obliquidens* in which such teeth are frequently encountered).

There is considerable variation in the number and disposition of inner rows. From 2–5 and from 2–4 series occur in the upper and lower jaws ; individuals with more than three rows usually have the interspace between outer and inner teeth greatly reduced or even absent, particularly in the upper jaw.

Lower pharyngeal bone sub-equilaterally triangular ; dentigerous surface slightly broader than long. Pharyngeal teeth similar to those described for *H. obliquidens.*

Osteology. That of a typical generalized *Haplochromis* species ; vertebrae 14 + 16 (in two specimens).

Coloration. Breeding colours of male *H. lividus* are perhaps the most distinctive morphological characteristic of the species and are not repeated or even approached in any other Lake Victoria *Haplochromis.* In preserved material their brilliance is lost. *Sexually active males.* Ground colour light olive-green shading to slate-grey ventrally ; flanks (including the dorsal aspects and in some, the nape) with a golden-red flush extending from the head to the caudal peduncle origin. Inter-orbital region of the head, the snout, lips and preorbital with a vivid, almost fluorescent, blue sheen, traces of which often extend onto the otherwise slate-grey lower jaw, lower preopercular limbs and the branchiostegal membrane. As far as can be determined, the intensity of this peculiarly intense head coloration is little influenced by the fishes' emotional state. On the other hand, its greatest extension is apparently manifest only in breeding fishes.

Dorsal fin grey to sooty, slight indications of fluorescent blue can be detected in some individuals ; red streaks on the posterior spinous and entire soft part ; lappets orange-red. Caudal dark, with ill-defined red maculae concentrated proximally on the upper half. Anal dark, with 2–4 yellow ocelli. Pelvics black, becoming lighter on the medial third. Coloration of *immature males* is similar except that the blue head colour is less concentrated and intense, or it may even be absent. The flanks are also less intensely red. *Females.* Ground colour light grey-green, becoming silver ventrally. Dorsal, caudal and pectoral fins colourless or faintly yellow-grey. Anal and pelvic fins yellow.

Preserved material : Males. Ground colour variable, usually grey. Dorsal caudal and anal fins clear or dark, the two former maculate as in life ; pelvics black. The blue head coloration is lost, but in most individuals it is faintly represented by a dead-white or ashen colour (at least in formalin fixed material preserved in spirit for five years). *Females and immature males.* Ground colour as above. All fins clear. From 5–7 transverse bars on the flanks ; the posterior pair rarely extend below the level of the lower lateral-line and are often joined by a short longitudinal stripe. Faint indications of a mid-lateral stripe are present in some individuals. Banding and striping are sometimes apparent in living fishes, but are intensified after death.

Distribution. H. lividus is known from several localities in Lake Victoria. (See below.)

Ecology : *Habitat.* Shallow littoral zone, especially in the vicinity of emergent and submerged vegetation, less frequently in the water-lily zone and at the margin of papyrus swamps; the species is commonly encountered over rock foundations of piers. Thus, the habitat preferences of *H. lividus* are similar to those of *H. obliquidens* with which species it is usually captured. There are, however, indications that *H. lividus* may inhabit the deeper littoral zone where *H. obliquidens* are relatively scarce.

Food. The intestine is long (2–2¼ times standard length) and much coiled; the stomach large and distensible. The stomach contents of sixty-two individuals (size range 56–90 mm. S.L.) from most localities have been examined. In general the food of *H. lividus* is similar to that of *H. obliquidens*.

Diatoms of the genera *Melosira* and *Rhopalodia* comprised the predominating digested contents in the stomachs of forty-five fishes, and were significant in twelve others.

Fragments of plant epidermis were found in thirty-three stomachs; as in *H. obliquidens* the amount and fragment-size showed considerable variation.

Filamentous green-algae, represented by *Spirogyra*, were recorded from only four fishes; in none was there any indication of digestion. Blue-green algae (especially *Rivularia* and *Microcystis*) were found in twenty-four stomachs. Again, the algae were apparently not digested.

Very fragmentary animal remains (Ostracoda, Crustacea [Decapoda] and Insecta [larval Chironomidae]) were recorded from sixteen individuals.

The occurrence of Insecta (winged Hymenoptera) as the main stomach contents in twelve fishes collected contemporaneously at one station, is of particular interest. Besides insect remains, diatoms were well represented in these stomachs. This observation suggests that *H. lividus* may feed facultatively on animal food at times of local abundance. Insects also comprised the main contents of two other specimens, both from different localities.

Feeding habits of *H. lividus* are probably similar to those of *H. obliquidens*. Direct observation shows the species to be a grazer on submerged plants and stones, whilst the occurrence of sand-grains and bottom debris in some stomach contents indicates occasional benthic feeding.

Breeding. Breeding habits and sites are imperfectly known. Three females carrying young in the buccal cavity have been collected; one from an exposed beach flanked by dense emergent vegetation and two from an off-shore water-lily stand. From one of these fishes twenty-five larvae of 12 mm. total length were recovered; the other females had jettisoned the greater part of their broods.

Affinities. Disregarding for the moment its peculiar male breeding coloration, *H. lividus* shows marked affinity with *H. astatodon*, *H. annectidens* and *H. obliquidens*, especially with regard to dental characteristics. Save *H. annectidens*, for which no information is available, the food of these species is similar, and composed mainly of epiphytic algae and plant debris (Poll and Damas, 1939, for food of *H. astatodon*).

In fact, *H. lividus*, *H. astatodon* and *H. annectidens* seem to provide examples of herbivorous intermediates linking generalized and usually insectivorous *Haplochromis* species with the specialized algal-grazer, *H. obliquidens*.

Within the species flock of Lake Victoria *H. lividus* shows some morphological relationship with *H. nuchisquamulatus*. Anatomical and dental characteristics might entitle *H. nuchisquamulatus* to consideration as the extant representative of an annectant form between *H. lividus* and the generalized species typified in Lake Victoria by *H. nubilus* (Blgr.) and *H. macrops* (Blgr.).

The present distribution of species having "*lividus*"-like teeth requires little comment. *Haplochromis astatodon* is endemic to Lake Kivu, whose *Haplochromis* species flock has long been recognized as having well-defined Victorian affinities (Regan, 1921), although the possibility of convergent evolution in the two lakes cannot be entirely discounted. *Haplochromis annectidens* is endemic to Lake Nabugabo and is part of a small species group which could only have been derived from that of Lake Victoria (Trewavas, 1933).

The presence within Lake Victoria of both *H. lividus* and its morphological derivative *H. obliquidens* is suggestive of an ancestor-descendant relationship. Before accepting this apparent phylogeny, due regard must be paid to the unique male breeding coloration of *H. lividus*. Baerends and Baerends van Roon (1950) expressed the opinion that male coloration plays an important part in species recognition amongst cichlids. Thus, we may assume the importance of male coloration as a barrier to interspecific mating. Field observations on the *Haplochromis* of Lake Victoria lend weight to this hypothesis. Although male colours and colour-patterns are broadly repeated in several species, no instance has yet been recorded of related species with identical or near identical male coloration breeding in the same habitat.

Therefore, although the distinctive coloration of *H. lividus* might be used in argument against close relationship with *H. obliquidens*, it might equally well be interpreted as resulting from selection strengthening mating barriers between species which occupy similar habitats, especially if the species are closely related and of recent origin.

Diagnosis. Haplochromis lividus differs from other *Haplochromis* in Lake Victoria in having distally compressed and expanded teeth whose crowns are unequally bicuspid and obliquely truncated. Dentition serves to distinguish this species from the fluviatile *Haplochromis* of East Africa. In life male coloration is the most obvious diagnostic character.

From species with similar dental morphology *H. lividus* may be differentiated as follows: from *H. astatodon* by its larger eye/cheek ratio; from *H. annectidens* by its slightly wider interorbital region and somewhat stouter, shorter teeth. In life coloration distinguishes *H. lividus* and *H. astatodon*; live colours are unknown for *H. annectidens*.

Five specimens from Lake Kyoga (*Tilapia nubila* B.M. (N.H.) reg. nos. 1911.3.3.141–145; 60–66 mm. S.L.) have teeth and dental patterns of the *H. lividus* type, but differ from Lake Victoria specimens in the following characters: dorsal head profile steeper; body deeper; and greater depth of cheek (23·3–25·2, mean 24·1 per cent head length). Should further collections from Lake Kyoga show that these fishes have *H. lividus* coloration (as is suggested in the preserved material) and should they also maintain the observed differences in morphology, then it will be necessary to recognize a distinct sub-species in that lake.

Study material and distribution records

Museum and reg. no.	Locality.	Collector.
British Museum (N.H.) 1906.5.30.318–320	Entebbe	Degen.
British Museum (N.H.) 1956.7.9.63–65	Jinja Pier	E.A.F.R.O.
,, ,, ,, ,, ,, ,, 58–62	Beach near Jinja	,,
,, ,, ,, ,, ,, ,, 66–74 (Type and paratypes)	Napoleon Gulf, near Bugungu (opp. Jinja)	,, ,,
,, ,, ,, ,, ,, ,, 75–83	Kirenia (near Jinja)	,,
,, ,, ,, ,, ,, ,, 84–94	Entebbe Harbour	,,
,, ,, ,, ,, ,, ,, 95–99	Beach near Nasu Point, Buvuma Channel	,, ,,
,, ,, ,, ,, ,, ,, 100–102	Hannington Bay (Uganda)	,,
,, ,, ,, ,, ,, ,, 103–124	Grant Bay (Uganda)	,,
,, ,, ,, ,, ,, ,, 125	Mwanza, Capri Bay	,,
,, ,, ,, ,, ,, ,, 126–128	Majita (Tanganyika Territory)	,,

Haplochromis nigricans (Blgr.) 1906

Tilapia nigricans (part) Blgr., 1906, *Ann. Mag. nat. Hist.* (7) **17**, 448; *Idem*, 1907, *Fish. Nile*, 518; *Idem*, 1911, *Ann. Mus. Genova* (3) **5**, 75; *Idem*, 1915, *Cat. Afr. Fish.*, **3**, 241, fig. 160.
Tilapia simotes Blgr., 1911, *Ann. Mus. Genova* (3) **5**, 75; *Idem.*, 1915, *op. cit.*, 242, fig. 161.
Neochromis nigricans (Blgr.), Regan, 1920, *Ann. Mag. nat. Hist.* (9) **5**, 33.
Haplochromis (*Neochromis*) *nigricans* (Blgr.), Regan, 1922, *Proc. zool. Soc., London*, 163.

As Regan (1922) first showed, Boulenger's figure of *Tilapia nigricans* is misleading. It was prepared from a specimen distorted in preservation and consequently the head profile differs considerably from that of *T. simotes*. However, in the important characters of dental pattern and morphology both species are identical. If the head of the figured specimen is restored to its natural position the characteristically decurved profile of *Haplochromis nigricans* is apparent.

Description. Based on fourty-four specimens (size range 49–94 mm. standard length) including holotypes of *T. nigricans* and *T. simotes*. Other specimens in the British Museum (Nat. Hist.) collections were examined but are not included in the morphometric data. The paratype of *T. nigricans* is clearly not referable to this species and should probably be placed in *H. lividus*. Its small size permits only tentative identification. Both skeletons in the British Museum (Nat. Hist.) are of *H. nigricans*.

Depth of body 34·5–40·0 (mean 36·9), length of head 28·0–33·3 (M = 31·2) per cent of standard length. Dorsal head profile strongly decurved. Preorbital depth 11·8–16·7 (M = 14·6) per cent of head length; least interorbital width 25·0–31·5 (M = 28·8); snout broader than long in most specimens of more than 65 mm. S.L., and as long as broad in smaller fishes, its length 26·3–35·2 (M = 30·4) per cent of head. Eye 25·9–33·3 (M = 30·0), depth of cheek 19·4–27·3 (M = 32·4) per cent of head.

Caudal peduncle from 1·1–1·8 (mode 1·3) times as long as deep, its length 11·4–17·6 (M = 15·4) per cent of standard length.

Mouth horizontal; posterior maxillary tip reaching the vertical from the anterior orbital margin or extending somewhat beyond. Jaws equal anteriorly, the lower short and broad, from 30·0–37·8 (M = 35·6) per cent of head length, its length/breadth ratio 1·0–1·4 (mode 1·2). *H. simotes* holotype is unusual in having its lower jaw only 28 per cent of the head length.

Gill rakers short, 8 or 9 (rarely 10) on the lower part of the first arch.

Scales ctenoid; lateral line interrupted, with 30 (f.1), 31 (f.12) 32 (f.28), or 33 (f.3) scales. Cheek with 2 or 3 (rarely 4) series of scales; 6 or 7 (less frequently 5 or 5½) between dorsal fin origin and the lateral line; 7 or 8 (rarely 6 or 9) between pectoral and pelvic fin insertions.

Fins. Dorsal with 24 (f.7), 25 (f.33) or 26 (f.4) rays, anal 11 (f.7), 12 (f.32) or 13 (f.5), comprising XIV–XVIII, 8–10 and III, 8–10 spinous and soft rays. First pelvic ray produced, extending to the vent or even to the soft anal; its posterior extension not correlated with sex or maturity. Pectoral fin shorter than the head. Caudal sub-truncate or feebly rounded; scaled on the proximal half to two-thirds.

Teeth. The outer series is composed of close set, movably implanted bicuspid teeth, with long, slender necks and expanded crowns. Cusp size in some individuals is markedly disparate, whilst in others the cusps are sub-equal. In the upper jaw, teeth situated postero-laterally are either tri- or unicuspid.

A weak positive correlation exists between the number of teeth in the outer series of the upper jaw and standard length.

S.L. (mm.)	49–58	59–68	69–78	79–93
Tooth number	40–50	46–60	46–60	54–70
Mean	46	52	52	62
N	19	6	14	4

The inner series is composed of small tricuspid teeth; 3–7 (mode 4) rows in each jaw. Compared with other Lake Victoria *Haplochromis* (except some individuals of *H. nuchisquamulatus* and *H. lividus*) the space separating inner and outer tooth series is greatly reduced in *H. nigricans*; it is non-existent in 30 per cent of the specimens examined.

Lower pharyngeal bone sub-equilaterally triangular; dentigerous surface somewhat broader than long; teeth numerous, and similar to those in *H. obliquidens* and *H. lividus.*

Cranial skeleton. The short and strongly decurved snout is reflected in the neurocranial shape. This differs slightly from that of generalized *Haplochromis* by having a more steeply sloping ethmo-vomer complex. Also, the dentary is relatively stouter and more massive in *H. nigricans.*

Coloration in life: Breeding males. Ground colour black, shot with metallic blue; snout, lips, interorbital region and to a lesser degree, cheeks and opercula, bluish. Dorsal fin black, lappets and maculae on the soft part deep crimson; anal dusky crimson, ocelli yellow; caudal crimson, pelvics black. *Adult females and juveniles.* Ground colour olivaceous; a faint golden-yellow flush over the opercula and branchiostegal membrane. Dorsal and anal fins dark yellow; caudal grey-green; pelvics dusky yellow.

Preserved material: Adult males. Black or slate grey; seven or eight transverse bars visible on the flanks of light coloured fishes. Dorsal fin black, with pale margin and maculae; caudal black proximally, pale distally; anal pale; pelvics black. *Females and juveniles.* Ground colour greyish-brown, with seven or eight dark transverse bars on the flank; a pronounced lachrymal stripe. All fins hyaline or slightly darkened.

Particular interest attaches to a single adult female with black and yellow piebald coloration similar to that described in *Macropleurodus bicolor* (Blgr.) and *Hoplotilapia retrodens* Hilgen. (Greenwood, 1956). The significance of this atypical individual is difficult to assess. In other characters *H. nigricans* does not manifest any apparent relationship with the monotypic genera, nor with *H. sauvagei* (Pfeffer), another species exhibiting sex-limited polychromism. It is probably the result of independent but parallel mutation occurring in *H. nigricans*, and therefore of no phyletic value. Such a phenomenon might be expected amongst members of a recently evolved and oligophyletic species flock.

Distribution. Lake Victoria and the Victoria Nile. Although most localities represented in the present collection are in Uganda, this should not be taken to indicate that *H. nigricans* is confined to, or more abundant in, these waters. The species has been seen in many areas, but its lithophilic habits render capture difficult except by unconventional or specialized gear.

Numerous specimens have been caught at Godziba Island (1° 29′ S., 32° 36′ E.). This small, rocky outcrop lies slightly south and west of the centre of Lake Victoria and is distant from either the mainland or other off-shore islands. Because there is no indication of *H. nigricans* ever occurring in deep or sub-littoral waters, one is led to suppose that Godziba fishes are at present isolated from coastal populations, and have been isolated for some considerable time. With this in mind, the Godziba sample was carefully compared with others from the mainland, but no phenotypic peculiarities could be detected.

Ecology: Habitat. H. nigricans is apparently confined to rocky and shallow areas of the littoral zone. Since rock exposures are not infrequent in the exposed littoral, its habitat, broadly speaking, overlaps that occupied by other algal-grazing *Haplochromis* species. No data are available for populations living in the Nile.

Food. The intestine is long (*ca.* 2½–3 times S.L.) and coiled. Observations on fishes in the lake indicate that *H. nigricans* feeds by grazing on algae from rock surfaces, a conclusion which is supported by stomach content analyses.

Ingested material from thirty-two stomachs showed a preponderance of diatoms over all other material. Specific identification of these plants was impossible, but the genera represented (chiefly *Navicula, Synedra, Rhopalodia* and *Gomphonema*) are typically epilithic or epiphytic in Lake Victoria (Ross, 1954). The absence, except from two stomachs, of fragmentary phanerogam tissue (an important element in stomach contents of other algal grazing species) was noteworthy, but explicable if *H. nigricans* graze from rock surfaces.

Filamentous green algae (*Spirogyra* and *Oedogonium*) and blue-green algae occurred less frequently, and were apparently undigested.

Very fine, sand-grain-like particles were recorded from thirteen stomachs. That these might have been fragments derived from rock surfaces and not the bottom seems likely in the absence of bottom debris typically associated with a sand substrate.

Breeding. Spawning sites are unknown. Courtship activity has been observed amongst fishes living over rocks near the Ripon Falls, but actual spawning was not seen. Two females have been found with embryos and larvae in the buccal cavity ; it is assumed that *H. nigricans*, like the generality of *Haplochromis* species, is a mouth-brooder.

The smallest adult fishes recorded were a female 51 mm. and a male 55mm. in standard length. Males apparently reach a larger size than females since no female greater than 70 mm. S.L. has been captured.

Affinities. Haplochromis nigricans is closely related to *H. serridens* Regan of Lake Edward (*vide* Trewavas, 1933). Both species have almost identical dental morphology and pattern, as well as similarity in general facies and preserved coloration. No clear-cut quantitative characters can be found to separate the species. There is, however, a subtle difference in their gross morphology, probably attributable to the more rounded physiognomy of *H. serridens*. Also, the inner tooth bands of this species are usually broader and possess more teeth than those of H. *nigricans*.

Tooth form, and less obviously the dental pattern, in one other Lake Edward species, *H. fuscus* Regan, is similar to that of *H. nigricans* ; but the species are readily distinguished by the smaller nuchal and thoracic scales in *H. fuscus* and also by its thicker lips and more abruptly declivous dorsal head profile.

Amongst Lake Victoria species *H. nigricans* is probably related to, and derived from a species resembling *H. nuchisquamulatus*.

Diagnosis. H. nigricans is distinguished from other Lake Victoria *Haplochromis* with bicuspid outer teeth by the following combination of characters : a short and broad lower jaw (modal length/breadth ratio 1 : 2) ; slender, movably implanted outer teeth narrowly separated, if at all, from the broad bands of inner teeth ; a strongly decurved dorsal head profile ; a long and convoluted intestine.

Study material and distribution records

Museum and reg. no.	Locality.	Collector.
British Museum (N.H.) 1906.5.30.469 (Holotype of *Tilapia nigricans*)	Entebbe .	Degen.
Genoa Museum (Holotype of *Tilapia simotes*) .	Kakindu (Victoria Nile) .	Bayon.
British Museum (N.H.) 1911.3.3.160–163 (Paratypes of *T. simotes*)	Jinja (Ripon Falls) .	Bayon
British Museum (N.H.) 1911.3.3.156–158, plus one additional specimen (Paratypes of *T. simotes*)	Kakindu .	Bayon
British Museum (N.H.) 1956.7.9.129–136 .	Napoleon Gulf, near Ripon Falls .	E.A.F.R.O.
,, ,, ,, ,, ,, ,, 137–148 .	Jinja Pier .	,,
,, ,, ,, ,, ,, ,, 149–150 .	Napoleon Gulf, near Jinja .	,,
,, ,, ,, ,, ,, ,, 151 . .	Beach near Nasu Point, Buvuma Channel .	,,
,, ,, ,, ,, ,, ,, 152 . .	Buka Bay (Uganda) .	,,
,, ,, ,, ,, ,, ,, 153–165 .	Godziba Island .	,,

Haplochromis nuchisquamulatus (Hilgendorf) 1888

Chromis nuchisquamulatus Hilgend., 1888, *S. B. Ges. naturf. Fr. Berlin*, 76.
Ctenochromis nuchisquamulatus (Hilgend.), Pfeffer, 1896, *Thierw. O. Afr. Fische*, 14.
Tilapia nigricans (part), Blgr., 1915, *Cat. Afr. Fish.*, **3**, 241.
Haplochromis nuchisquamulatus (part), *idem*, *ibid.*, 290.
Haplochromis (*Neochromis*) *nuchisquamulatus* (Hilgend.), Regan, 1922, *Proc. zool. Soc., London*, 163.

The holotype of *H. nuchisquamulatus* is amongst those specimens, once housed in the Berlin Museum, which cannot be located at the present time. It is thus the more regrettable that Hilgendorf's original description is totally inadequate for modern taxonomic purposes.

As a basis for comparison I have therefore relied upon Regan's identification of two British Museum (Nat. Hist.) specimens. From Regan's paper (1922) it is clear that he, too, was unable to study the type specimen, but he apparently gained sufficient information from photographs and data supplied by Dr. Pappenheim to identify his material. Of this I have located only one specimen (British Museum (N.H.) reg. no. 1911.3.3.155, from Kakindu, Victoria Nile). In its general morphology this fish agrees closely with a photograph of the type. Further, with the aid of a binocular microscope it has proved possible to check certain other characters visible in this remarkably clear photograph.[1]

Although this species is represented in my study-material by only six specimens, I have little doubt as to its biological validity. Morphologically *H. nuchisquamulatus* is intermediate between *H. lividus* and *H. nigricans*: it may well represent the stock from which these species diverged. The tooth form of *H. nuchisquamulatus* is less specialized than that of *H. lividus* and is nearer *H. nigricans*. That is to say, the outer teeth are slender, bicuspid and movable, whilst those of the inner series show a tendency towards an increase in the number of rows and a decrease in the space separating them from the outer series. The lower jaw is more slender than in *H. nigricans* and is similar to the dentary in *H. lividus* and *H. obliquidens*, and in other, more generalized *Haplochromis*.

None of the dental and associated characters considered above lies within the known range of intra-specific variability for *H. nigricans* or *H. lividus*. Neither is there any indication by analogy with well-defined *Haplochromis* species that the "*nuchisquamulatus*" character-complex is an extreme variant of some other species

Description. The principal morphometric characters for each of the six specimens examined are tabulated below. All are adult males.

S.L.	Depth.*	Head.*	Po. %	Io. %	Snt. %	Eye. %	Ch. %	Lj. %	C.P.*
83·0	38·0	31·3	15·4	30·8	30·8	30·8	23·0	36·5	15·7
86·0	37·2	32·5	14·3	28·6	28·6	32·2	23·2	35·7	15·2
93·0	38·7	32·3	14·5	29·0	32·2	29·0	24·2	38·6	15·1
98·0	38·8	31·6	16·2	30·0	32·2	25·8	22·6	38·7	15·3
99·0	37·4	32·8	15·4	30·8	30·8	30·8	24·6	40·0	15·2
113·0	37·0	30·3	17·4	26·5	31·8	29·0	26·5	36·2	18·6

* Percentage standard length.
% Percentage head-length.

---

[1] To be reproduced in a later part of this series.

Dorsal head profile curved and sloping. Mouth horizontal; posterior maxillary tip extending to the vertical from the anterior orbital margin or slightly beyond. Jaws equal anteriorly, the length/breadth ratio of the lower 1·4–1·7 (mode 1·5).

Teeth. Outer teeth unequally bicuspid; a few slender and unicuspid teeth occur posteriorly in the upper jaw, in which there are from 50–70 teeth. Although relatively fine, the neck in these teeth is stouter and less clearly demarcated from the expanded crown, than in *H. lividus* or *H. obliquidens.*

Inner teeth small and tricuspid, occurring in 4–8 and 3–6 rows in the upper and lower jaws respectively; the space separating inner and outer series is reduced.

Lower pharyngeal bone sub-equilaterally triangular, its dentigerous surface slightly broader than long. Teeth fine and numerous; in the three larger specimens, the median teeth are enlarged.

Gill rakers short, 8–10 on the lower part of the first arch.

Scales ctenoid: lateral line interrupted, with 31 (f.2), 32 (f.2) or 33 (f.2) scales. Cheek with 2 or 3 series. 6–8 scales between dorsal fin origin and the lateral line; 6–8 scales between pectoral and pelvic fin insertions.

Fins. Dorsal with 24 (f.1), 25 (f.2) or 26 (f.3) rays, anal 12 (f.4) or 13 (f.2), comprising XV–XVII, 9 or 10 and III, 9 or 10 spinous and soft rays. First pelvic ray produced, extending to the second anal ray. Pectoral fins slightly shorter than the head. Caudal sub-truncate.

Skeleton. That of a generalized *Haplochromis.*

Coloration. Unknown in life and known only for preserved males. Ground colour dark greyish-brown, the dorsal and ventral surfaces darker than the flanks, across which seven transverse bars are visible; in two specimens the chest is black. Well-defined, narrow lachrymal and two interorbital stripes; two broad bands across the nape, one immediately post-ocular in position, the other slightly more posterior.

Ecology. Of the six specimens studied, five were caught in exposed littoral zones of Lake Victoria, and one in the Victoria Nile. The type specimen is from Lake Victoria, but no precise locality is given.

Food. Fragments of plant tissue and numerous epiphytic algae were recorded from four of the five stomachs examined, whilst the fifth contained filaments of *Oedogonium* and some fragmentary plant tissue.

Diagnosis. H. nuchisquamulatus is distinguished from other Lake Victoria *Haplochromis* with bicuspid outer teeth by the following combination of characters: long and convoluted intestine (*ca.* 3 × S.L.); relatively slender, movably implanted and numerous outer teeth; increased number of inner tooth rows (3–8) narrowly separated from the outer series. From *H. nigricans* it is recognized by the narrower lower jaw and less strongly decurved dorsal head profile; outer teeth in *H. nuchisquamulatus* are also somewhat stouter than those of *H. nigricans.* These acutely cuspidate teeth serve to separate *H. nuchisquamulatus* from *H. lividus.*

The diagnostic character used by Hilgendorf (small nuchal scales whose exposed surface is less than half that of flank scales) cannot be considered valid. In most *Haplochromis* nuchal scales are smaller than those on the flank, and furthermore are subject to quite considerable intra-specific size-variation.

Study material and distribution records

Museum and reg. no.	Locality.	Collector.
British Museum (N.H.) 1911.3.3.154	Kakindu (Victoria Nile)	Bayon.
British Museum (N.H.) 1906.5.30.316–317	Entebbe	Degen.
British Museum (N.H.) 1956.7.9.166–167	Beach near Nasu Point, Buvuma Channel	E.A.F.R.O.
,, ,, ,, ,, ,, ,, 168	Godziba Island	E.A.F.R.O.

SUMMARY

1. The algal-grazing species *Haplochromis obliquidens* Hilgendorf 1888, *H. nigricans* (Boulenger) 1906, and *H. nuchisquamulatus* (Hilgendorf) 1888, are redescribed on the basis of new and more extensive collections.

2. A new species, *H. lividus*, apparently related to *H. obliquidens* is described.

3. Data on the food and ecology of these species are given.

4. Consideration is given to the possibility of recognizing a number of supraspecific groups of *Haplochromis* in Lake Victoria. At present, although such groups may be determined, it is impossible to give them formal taxonomic status.

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A SYSTEMATIC REVISION OF THE FISHES OF THE TELEOST FAMILY CARAPIDAE (PERCOMORPHI, BLENNIOIDEA), WITH DESCRIPTIONS OF TWO NEW SPECIES

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D. C. ARNOLD

(Gatty Marine Laboratory, and Department of Natural History, St. Andrews)

Pp. 245–307 ; 20 *Text-figures.*

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A SYSTEMATIC REVISION OF THE FISHES OF THE TELEOST FAMILY CARAPIDAE (PERCOMORPHI, BLENNIOIDEA), WITH DESCRIPTIONS OF TWO NEW SPECIES

By D. C. ARNOLD

SYNOPSIS

The life history, mode of life and behaviour of *Carapus acus* (Brünnich) are briefly reviewed and compared with those of other species. An account of the range of skeletal structure within the Carapidae is given as a basis for generic separation, the various species are redescribed and their synonymies are revised. Two new species of the genus *Carapus* are described. Keys are given for the diagnosis of the genera, subgenera and species recognized. The paper is illustrated by 20 text-figures and includes a list of the principal references to the family Carapidae.

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I. INTRODUCTION

The best known member of the Carapidae is the Mediterranean species *Carapus acus* (Brünnich), a monograph on which was published over seventy years ago (Emery, 1880). This account was principally devoted to the adult anatomy, but also included observations on the life history and behaviour of the fish. Other members of the family have been briefly recorded in a number of ichthyological works, but no general account of the family appears ever to have been published.

The work here recorded was performed mainly in Italy and at Plymouth. Studies on living fish were undertaken during tenure of the Oxford and Royal Society Tables at the Stazione Zoologica, Naples, while the taxonomic portion of the work was performed almost entirely during tenure of the Oxford Table at the Laboratory of the Marine Biological Association of the United Kingdom, Plymouth. Short periods were also spent in study at the British Museum (Natural History) and at the Scottish Home Office Laboratory, Aberdeen.

Preserved specimens were obtained from certain other sources, notably from the following institutes :

Universitetets Zoologiske Museum, Copenhagen.
Institut Océanographique, Monaco.
Museu Municipal, Funchal, Madeira.
Institut za Oceanografiju i Ribarstvo, Split.

Information on the distribution of various species was obtained by correspondence with the following laboratories :

Institut d'Hydrobiologie et de Pêche, Alexandria, Egypt.
Marine Biological Station, al Gardaqa, Egypt.
Institut Scientifique Chérifien, Rabat, Morocco.
Laboratorio Oceanográfico, Malaga, Spain.
Station Biologique, Roscoff, France,
Station Biologique, Archachon, France.
Institut za Biologiju Mora, Rovinj, Yugoslavia.
Zoology Department, University College, Achimota, Gold Coast.
East African Marine Fisheries Research Organization, Zanzibar.
The University, Travancore, India.
Fisheries Department, Penang, Malaya.
Department of Agriculture, Sandakan, North Borneo.
Department of Harbours and Marine, Brisbane, Australia.
Department of Zoology, The University, Sydney, Australia.
Victoria University College, Wellington, New Zealand.
Department of Zoology, The Museum, Dunedin, New Zealand.

Radiographs of representative specimens were made by the Radiography Department of the Royal Naval Hospital, Devonport, and of type material by Mr. A. C. Wheeler of the British Museum (Natural History).

My most grateful thanks are due to the Directors and Staffs of these various institutions, without whose kindly co-operation and assistance this work would not have been possible and to the many individual workers with whom I have discussed the results of this investigation and the problems arising therefrom.

During the course of this study financial support was provided by the Oxford Naples Scholarship and by a maintenance grant and supplementary grants from the Department of Scientific and Industrial Research.

II. THE LIFE HISTORY OF *CARAPUS ACUS*

Eggs attributable to *C. acus* are found in the Mediterranean during July, August, and early September, floating at the sea surface in yellowish, oval masses each containing some thousands of eggs. The egg is ellipsoidal, with diameters of 0·90 mm. and 0·75 mm., and has a large oil-globule, the yellowish tint of which is responsible for the colour of the egg-rafts (Raffaele, 1888). Spawning has not been observed, not has artificial fertilization been achieved. Embryonic development is rapid, the larva hatching in an anatomically incomplete condition on the third day after spawning. Emery described the early development in general terms, but owing to the paucity of material the embryology of the fierasfers has never been subjected to critical study by modern methods.

At hatching, the young fish enters the first larval stage, the vexillifer, characterized by a long dorsal appendage, the vexillum. On the first day of post-embryonic life this appendage is a small, pigmented thickening at the anterior end of the dorsal fin, but as the larva grows the thickening enlarges, forming first a small papilla, then a soft, forked projection and finally a long, lobed structure whose size and complexity increase with the increasing size of the larva (Emery, 1880). As the vexillum grows, its pigment is limited first to the lobes and then to their proximal portions, leaving the stalk and distal parts of the lobes relatively unpigmented in the older larvae. Later still the vexillum degenerates and the larva sinks from the surface into the deeper layers until finally, with the appendage reduced to a mere projection or even lost entirely, the young fish enters upon the benthic mode of life of the second carapid larva. It is probable that regression does not often run its full course, for the fragility of the vexillum is such that few fish are obtained with it undamaged and it must often be broken off instead of resorbed.

Emery hatched fierasfer larvae in the aquarium and reared them for about a week, but was unable to feed the fish and could not follow their development after they had attained a length of 3–4 mm. Further knowledge of the growth and metamorphosis of the vexillifer has been obtained solely from specimens taken in plankton hauls, most of which were never studied alive. The youngest vexillifers taken in the plankton were a pair obtained by Emery. They were about 10 mm. long, but showed little advance on those he was able to rear. Others studied by Padoa (1947) ranged from 15 mm. to 85 mm. in length. From this author's account it appears that increase in size is unaccompanied by any great changes in proportion. The head remains approximately one-fifteenth of the total length, the preanal length about one-tenth of the total, while throughout the vexillifer stage the end of the abdominal cavity is only a short distance behind the anus. A 76 mm. vexillifer mentioned by Emery agrees well with Padoa's series, as do the large specimens described by Gasco (1870) and Costa (1871) under the name *Vexillifer dephilippii* Gasco.

The second larval stage of *C. acus* is at first benthic, later inquiline. It was originally described as *Encheliophis tenuis* Putnam (1874) and Padoa (1947) has proposed that it be termed the tenuis larva. The tenuis has been found far less frequently than has the vexillifer and records of perhaps not more than 20 have appeared in the literature.

The tenuis stage is essentially a phase of growth and change. It lacks the vexillum and is characterized principally by the immense length of the cylindrical body and the relative smallness of the head. In the later vexillifers the head comprises about one-fifteenth of the total length, yet in the youngest tenuis so far described (Emery, 1880) the head constituted but one-thirtieth of the total and its actual length, 5 mm., was no greater than that of the head of a vexillifer of only half its size.

While the tail is elongating, the head and trunk of the tenuis are also growing, though not nearly so rapidly. Thus the disparity between head and trunk length on the one hand and total length on the other continually increases. At a total length of about 200 mm. further changes occur. Elongation is now replaced by shortening ; tail growth by tail resorption. But though the tail region of the tenuis now decreases in length, the head and trunk regions continue to grow and the proportions of the body approach ever more closely to those of the adult fish. However, even in the anterior region of the body not all parts develop alike, for while the head and abdominal cavity elongate, the anus remains at about the same distance from the snout and thus occupies an ever more advanced position. During this and subsequent stages of development the depth of the body also increases, though the width remains fairly constant, and the cylindrical body of the tenuis is converted to the compressed form of the adult fierasfer.

The tenuis lacks pigment except for the silvery iris and black and red chromatophores on the top of the head. Trunk and tail are glassily transparent. When removed from a holothurian, the tenuis has a pinkish tinge which fades after a short time in sea water and is never recovered. It is apparently due to the colour of the blood.

The tenuis does not metamorphose directly into the adult, but into a well-marked juvenile stage (Arnold, 1953). This is primarily a period of consolidation in which the developmental trends of the tenuis are continued to produce the adult form. At the close of metamorphosis the head of the young fish is about one-twelfth of the total length ; the anus is beneath, or only a little behind, the vertical through the roots of the pectoral fins ; the pectorals are round and short, one-quarter to one-third the length of the head ; and patches of black pigment have begun to appear on the still translucent tail.

At first the total length, 70–80 mm., alters but little, though the head continues to elongate and the trunk to deepen. When the adult proportions have been nearly obtained and the length of the head is between one-seventh and one-eighth of the total length, the fish elongates once more. Now, however, all parts of the body grow at about the same rate and there is little further alteration in proportions, beyond a deepening of the anterior part of the trunk and the advancement of the anus to a position a little in front of the pectoral fins. The changes in length of head relative to total length during the life history of *C. acus* are shown graphically in Text-fig. 1. As growth proceeds, the pectorals elongate, becoming oval and about one-half the length of the head, while red chromatophores appear among the black. The reddish tinge given to the body marks the end of the juvenile stage and may perhaps be associated with the onset of sexual maturity. Behavioural changes also occur at this time.

The dentition of the developing *C. acus*, owing to the importance of dental characters in the identification of adult fierasfers, deserves special consideration. The smallest vexillifers lack teeth, but in later individuals teeth appear on jaws, palatines and vomer. These teeth are at first uniserial in arrangement and of uniform size, but as the vexillifer grows a pair of rather larger teeth appears at the front of the upper jaw, followed by a similar pair in the lower jaw, and both pairs are fully developed by the time that a total length of 60 mm. has been attained (Padoa,

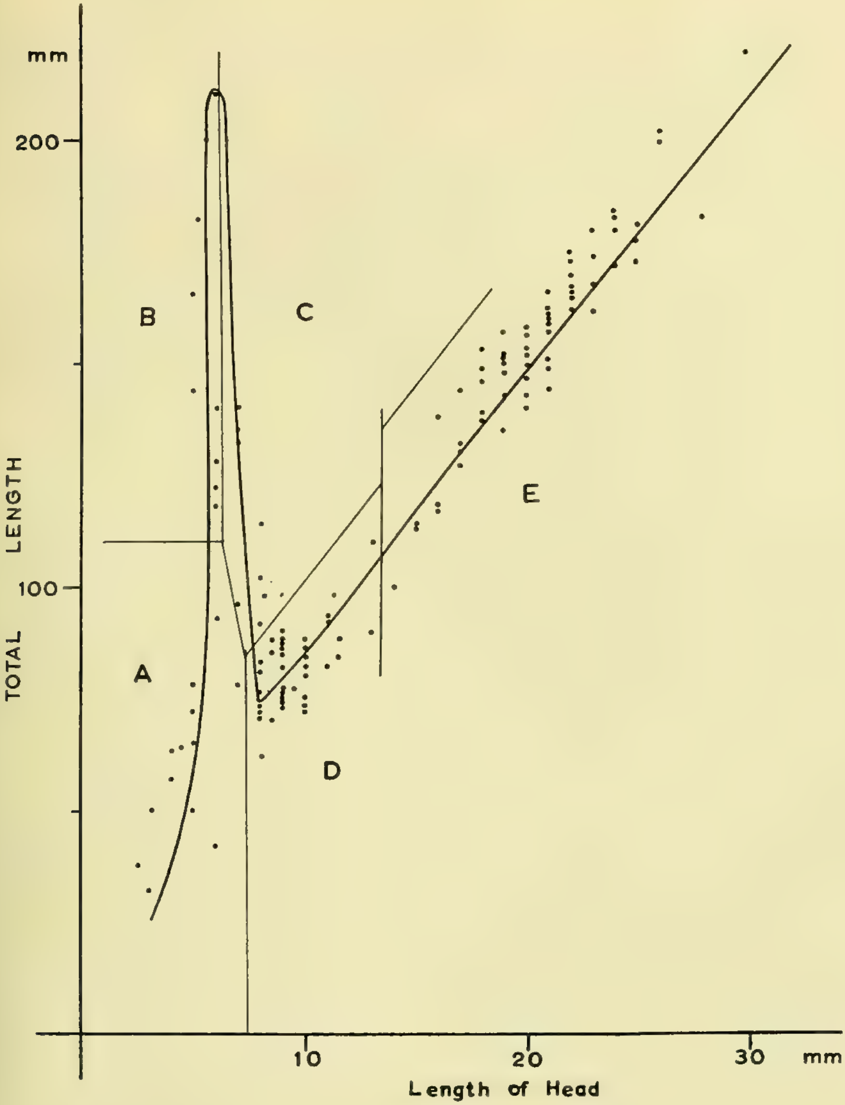


FIG. 1.—Changes in proportions (head length relative to total length) during the life history of *Carapus acus*. A, Vexillifer; B, early tenuis; C, late tenuis; D, juvenile; and E, adult stages.

1947). Towards the end of the vexillifer stage the size difference between these anterior teeth and those in the rest of the jaw diminishes and towards the close of the tenuis stage enlarged anterior teeth are no longer present. Throughout the tenuis period the dentition remains uniserial on jaws and palatines, but at the beginning of the juvenile stage the number of rows begins to increase until the completely polyserial condition of the adult is attained.

It has been suggested (Dean, 1895) that the elongated bodies of the fierasfers, their persistent notochord and functional pronephros are expressions of a general paedomorphic tendency of the family and it is probable that the dental characters of many species, the enlarged anterior jaw teeth of certain *Carapus* spp. and the uniserial dentition of *Encheliophis*, are also larval characters perpetuated in the adult form. In the circumstances, considerable doubt is cast upon the validity of the dentition as a diagnostic character for the separation of new species unless it can clearly be shown that the types are mature individuals, while the occurrence of partially uniserial dentition in a fierasfer of small size can probably always be taken as indicating that the specimen in question is in the juvenile stage of its development.

III. BEHAVIOUR AND MODE OF LIFE

The behaviour of the adults of *Carapus acus* was first studied by Emery (1880), who found that the fish swam in a sharply-tilted, head-down position and entered the host holothurian tail-first through the anus. Recent observations on the same species (Arnold, 1953) have shown pronounced behavioural differences between fish in different stages of the life history. The youngest specimens of *C. acus* studied alive were tenuis larvae obtained from *Holothuria tubulosa*. When removed from the host and placed in sea water they showed a characteristically violent movement. The body was slanted upwards, the head even thrust above the surface of the water, and its flexures were of extremely wide amplitude, very different in appearance from the normal swimming movements. Such " tenuis " movements were occasionally shown by juveniles and adults when removed from their hosts or when attempting to evade capture. Fish displaying " tenuis " movements did not respond in any way to the presence of a holothurian, nor did the tenuis larvae themselves appear to be capable of entering a new host. Juveniles and adults, however, responded at once to the presence of a holothurian and would swim the length of its body until they located the anus, then attempt to enter. Adults almost always entered tail-first by means of a pronounced corkscrew motion in which the body of the fish rotated through 360° or more. The juveniles normally entered head-first, though some of the older specimens might make incomplete and unsuccessful attempts at a tail-first entry. Only those fish which had attained their full growth in the juvenile condition and were beginning to assume the form and colour of the adult displayed both modes of entry.

Behaviour differences such as these may be shown also by other fierasfers, but at present the few recorded observations on other members of the Carapidae relate almost entirely to adult fish. Tail-first entry has been described for the adults of *C. bermudensis* (Jones) (Linton, 1907 ; Aronson & Mosher, 1951) and *C. homei*

(Richardson) (Mukerji, 1937). The entry of *Encheliophis gracilis* (Bleeker) into starfish has been observed (Doleschall, 1861), but it is not clear from this account whether entry was head-first or tail-first. *Encheliophis hancocki* (Reid) has been observed both to enter and leave its host head-first (Steinbeck & Ricketts, 1941). Nothing whatsoever is known of the behaviour of those species which inhabit lamellibranchs.

Most accounts of the behaviour of fierasfers have been purely descriptive and little attempt has been made to analyse the behaviour of any species in terms of stimuli and responses. Studies on adults and juveniles of *C. acus* by means of various models showed that the fish responded only if the water contained mucus from a holothurian and provided that the model was long relative to its depth (Arnold, unpublished observations). In the absence of a chemical stimulus *C. acus* shows none of the exploratory movements that usually precede attempt at entry, while an ovoid or circular model is usually ignored. Presence of a water current seems to be a necessary prerequisite for actual penetration, though in the absence of prior chemical and visual stimuli a water current alone has either no effect or is actually repellent to the fish. Recent work on *C. bermudensis* has shown that in this species chemical and tactile stimuli are of most importance (Aronson & Mosher, 1951), but a full account of this work has yet to be published.

C. acus lies within the body cavity of its host, usually at the anterior end among the branches of the gonads, on which it apparently feeds. The tenuis larva does not survive long after removal from its host and the fierasfer must thus remain within its first holothurian throughout this period of its life history. Juveniles and adults live well in sea water and small crustacea have been found among their stomach contents. It is probable that *C. acus* leaves its host only when the holothurian eviscerates.

Little is known of the location of other fierasfers within the bodies of their hosts. *Encheliophis gracilis* apparently breaks into the body cavity of the starfish it inhabits (Doleschall, 1861 ; Yosii, 1928), and *Encheliophis vermicularis* Müller has been found within the body cavity of its host holothurian, feeding upon the viscera (Semper, 1861). Both *Encheliophis hancocki* and *C. bermudensis* have been observed freely to enter and leave their hosts (Steinbeck & Ricketts, 1941 ; Linton, 1907) and thus can hardly have penetrated further than the cloaca or base of the branchial trees. Different species of fierasfer doubtless differ in their dependence upon their hosts and in the distance to which they penetrate into the body.

Some fierasfers seem to show little host specificity. *C. homei*, for example, has been recorded from holothurians, asteroids, echinoids, lamellibranchs and a tunicate. Others however, are restricted to particular host species. Thus *C. bermudensis* has been recorded only in *Actinopyga agassizi*, *Encheliophis sagamianus* (Tanaka) only in *Holothuria monacaria*, and *C. acus* only in *H. tubulosa* and *Stichopus regalis*. In the laboratory *C. acus* also enters *H. poli*, *H. helleri* and *H. sanctori*, but does not respond to *Cucumaria planci* or *Phylloporus urna*. It does not penetrate into the body cavity of *H. poli*, but lodges in the branchial trees and usually emerges within 24 hours. Choice experiments did not provide evidence that *C. acus* could distinguish between *H. tubulosa* and *H. poli* prior to entry.

IV. STRUCTURE

A full account of the structure of the commonest European fierasfer, *Carapus acus*, was given by Emery (1880), but little is known of the anatomy of any other species. Owing to the general rarity of the fierasfers it has been impossible to make a comparative study of their soft anatomy, but X-ray examination of a number of the types and of other clearly identifiable specimens has enabled the skeletons of a number of species to be studied without damage to the specimens themselves. In all species examined the tail and posterior trunk vertebrae have been found to possess the same general characters, differing only in size and relative degree of ossification. The centra are characteristically hour-glass shaped, generally twice as long as wide or high, and surmounted by long, pointed, backwardly directed neural spines which in the trunk region project above the succeeding vertebrae, but in the tail region become progressively smaller until towards the tip of the tail they are no longer recognizable. The transverse processes of the trunk vertebrae jut out at right angles from the centra, then turn downward and backward. The haemal spines of the tail vertebrae are extremely long anteriorly, but decrease in height towards the tip of the tail. In this region ossification becomes so slight that it is usually impossible to count the total number of vertebrae, the most posterior of which are mere rings encircling the persistent notochord.

But though the various species resemble each other in the form of the majority of their vertebrae, in the structure of the anterior vertebrae and of the lower jaw they are classifiable into three sharply separated groups, two of which may be further subdivided by means of other characters. In the systematic portion of this account, this subdivision of the Carapidae on the basis of skeletal characters has been used as the basis for generic separation of the adults. Though it has not been possible to examine the skeletal characters of larval fierasfers, the lower jaws (which can easily be seen by superficial examination) show similiar variations to the lower jaws of adults and thus provide grounds for generic classification even of immature specimens.

The majority of fierasfers examined—including representatives of the species originally described as *Gymnotus acus* Brünnich, *Fierasfer dubius* Putnam, *Lefroyia bermudensis* Jones, *Oxybeles Homei* Richardson, *Fierasfer parvipinnis* Kaup, *Fierasfer affinis* Günther, *Fierasfer caninus* Günther, *Fierasfer margaritiferae* Rendahl and *Carapus parvibrachium* Fowler—form a fairly homogenous group which in the main corresponds with the genus *Carapus* as at present understood. The majority of these species have 17–18 trunk vertebrae (19–20 in *Fierasfer margaritiferae* and *Carapus parvibrachium*), the first of which has a roughly cubical centrum surmounted by a stout neural spine with a truncated tip. This spine slopes forward and appears to be attached to the skull by a calcified ligament. The transverse processes of the first vertebra are slender and scimitar-shaped, directed backward and downward. The second vertebra resembles the first in the form of its centrum and transverse processes, but has a pointed neural spine which slopes slightly backward. The third and fourth vertebrae have hour-glass shaped centra, long backwardly-projecting neural spines and expanded transverse processes which are fused together into broad

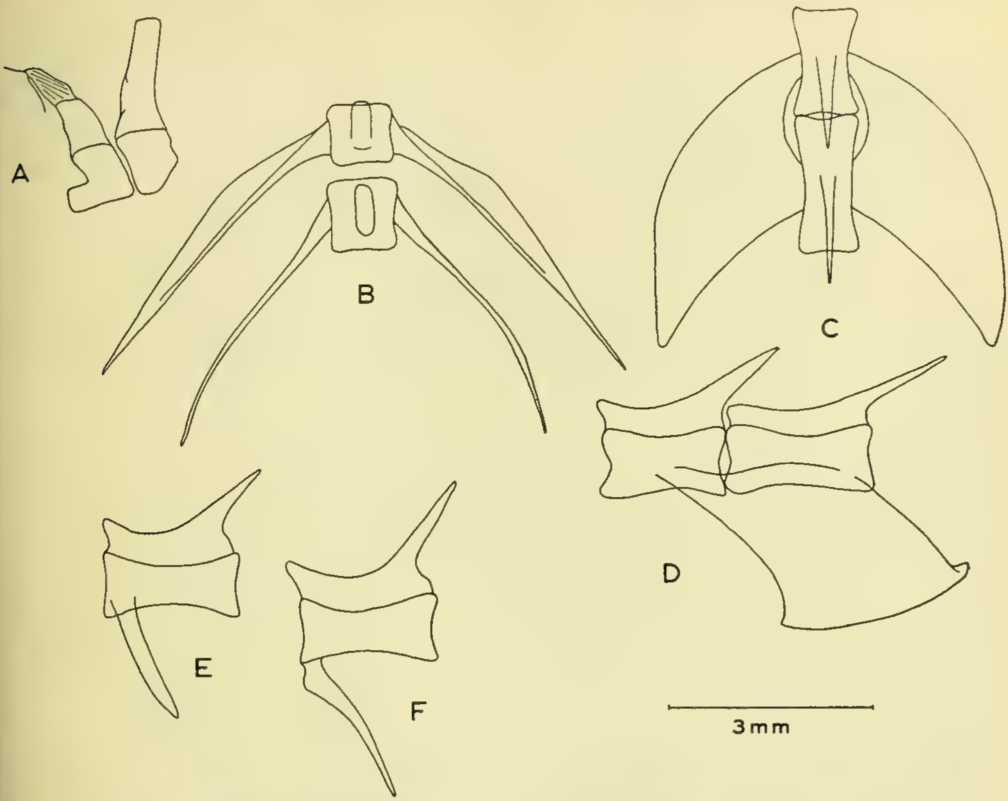


FIG. 2.—Vertebrae of *Carapus acus*. A, Nos. 1 and 2, lateral aspect (transverse processes omitted) ; B, nos. 1 and 2, dorsal aspect ; C, nos. 3 and 4, dorsal aspect ; D, nos. 3 and 4, lateral aspect ; E, representative posterior trunk vertebra ; F, representative anterior tail vertebra. (*Camera lucida* drawings from radiographs.)

flat plates, rounded anteriorly and tapering posteriorly to points level with the middle of the fifth vertebra (Text-fig. 2).

In this group of fierasfers the lower jaw is nearly flat along its lower edge. The upper tooth-bearing edge commences parallel to the lower, then curves upwards to the greatly expanded proximal portion of the jaw (Text-fig. 3A). The narrowest part of the jaw is the extreme tip, from which a lateral ridge, parallel to the lower edge, extends to the point of articulation with the cranium. Just beneath this ridge there is at the distal extremity of the jaw a deep and narrow notch. The teeth are in a narrow band (a single row only in the larvae) along the entire exposed surface of the jaw. Each tooth is separated from its neighbours by a space almost as wide as the diameter of the base of the teeth.

Two of the species included within this group, *Fierasfer margaritiferae* and *Carapus parvibrachium*, could not be examined in such detail as the rest owing to the presence of a large reniform, calcareous body lying in the midline in the anterior part of the body. This structure, presumably the anterior part of the swim-bladder, effectively concealed parts of the second, third and fourth vertebrae. So far as they could be seen, however, they appeared similar in general structure to those of of the other species, though undoubtedly differing in detail. These two species differ also from the others in their slightly greater number of trunk vertebrae and in certain aspects of their dentition. In the systematic account they are therefore accorded subgeneric status.

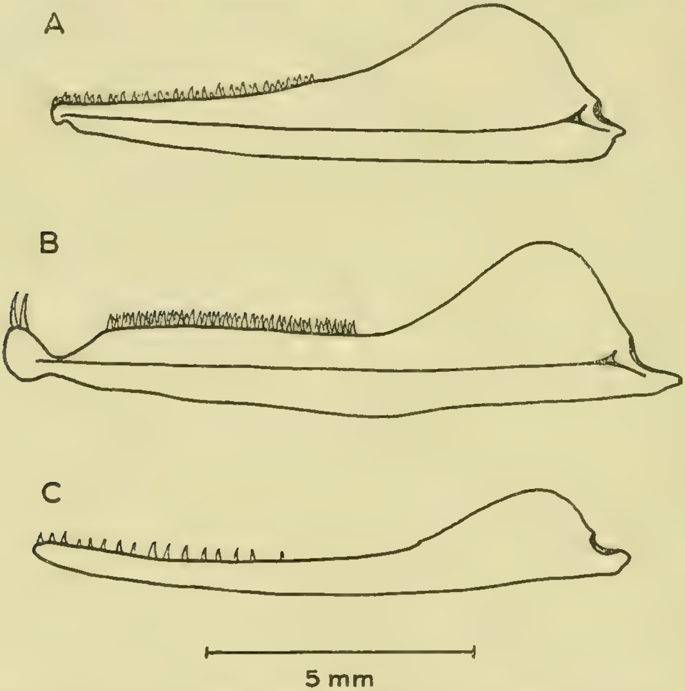


FIG. 3.—Jaw structure in the Carapidae. Lower jaws of A, *Carapus* ; B, *Echiodon* ; and and C, *Encheliophis*. (Semidiagrammatic drawings based upon radiographs.)

The second group of fierasfers contains only two species which have been available for examination, those originally described as *Ophidium dentatum* Cuvier and *Echiodon Drummondi* Thompson. These species have been frequently confused with each other and generally assigned to *Carapus*. Both in structure and appearance, however, they differ considerably from the group of species so far considered. The body is considerably longer and the trunk region of the vertebral column comprises 27–28 vertebrae, the first two of which are similar to the first two of the species already considered. The third and fourth vertebrae, in contrast, are entirely separate from each other and show not the least sign of fusion of the transverse processes (Text-fig. 4). The edges of the lower jaw are flat and parallel, the proximal portion is small and at its tip the jaw first narrows, then expands again as a small knob (Text-fig. 3B). A lateral ridge runs from this knob, across the narrowed portion of the jaw and as far as the articulation with the skull. The dentition comprises two series. Anteriorly one or two immense, fang-like teeth occupy the terminal knob, while the neck is toothless and its position easily visible in the intact animal as a pronounced diastema. The rest of the jaw is occupied by a narrow band of teeth (or single row only in the larva) closely pressed together.

Composing the third group of fierasfers is a number of species which, judged externally, appear to fall into two classes. Examples of the species originally described as *Oxybeles gracilis* Bleeker and *Encheliophis vermicularis* Müller have been studied. Of these, *E. vermicularis* lacks pectoral fins though the girdle is still present, while specimens of *O. gracilis* are individually more robust and possess small pectorals. In vertebral and jaw structure, however, *O. gracilis* and *E. vermicularis* are almost identical. There are 30–31 trunk vertebrae, the first two of which resemble those already described for the first group of fierasfers, with the exception that the neural spine of the second vertebra is rather shorter and stouter and is attached to the back of the skull by a structure which is apparently a slender, calcified ligament. The insertion of this ligament spreads on to the anterior part of the neural arch of the third vertebra (Text-fig. 5). It is characteristic of this third group of fierasfers that the third, fourth and fifth trunk vertebrae have their transverse processes expanded and fused into wide lateral wings, the outer edges of which are smoothly curved, while their points reach as far back as the level of articulation between the sixth and seventh vertebrae.

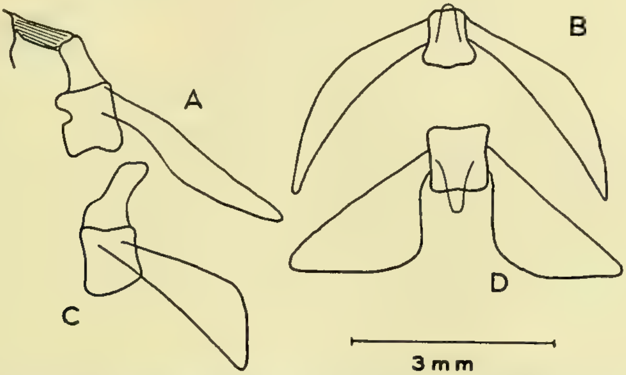


Fig. 4.—Vertebrae of *Echiodon drummondi*. A, No. 1, lateral aspect; B, no. 1, dorsal aspect; C, no. 2, lateral aspect; and D, no. 2, dorsal aspect. (*Camera lucida* drawings from radiographs.)

O. gracilis and *E. vermicularis* differ from all other fierasfers in the slender, curved form of the lower jaw. The narrowest portion is at the tip, the proximal part is little expanded and the lateral ridge is little developed (Text-fig. 3C). Even in the adult the teeth are in a single row only and are widely separated from each other, the distance between successive teeth being as much as two or three times the diameter of the tooth-base.

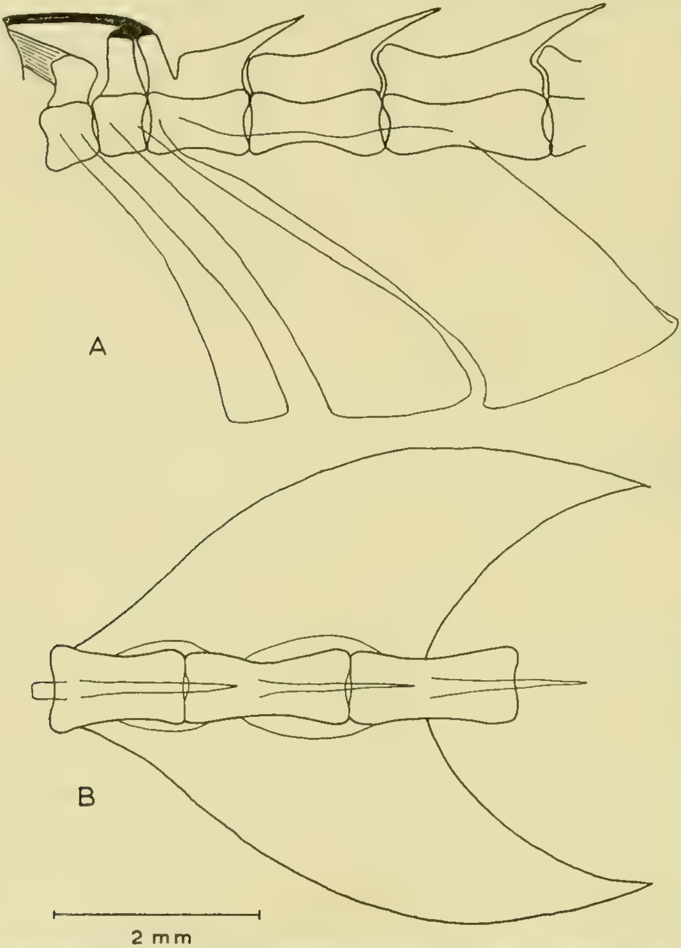


FIG. 5.—Vertebrae of *Encheliophis* (*Jordanicus*) *gracilis*. A, Nos. 1–5, lateral aspect; B, nos. 3–5, dorsal aspect. (*Camera lucida* drawings from radiographs.)

Various characters have been used for the discrimination of species within the Carapidae, but those which have proved most generally useful for diagnosis are the dentition and certain proportions of the body. Owing to their soft bodies, fierasfers are liable to shrinkage and distortion on preservation and in the following systematic description all measurements have been made on specimens preserved either in formalin or, more usually, in alcohol. In order to determine the effect of post-mortem shrinkage and to enable these measurements to be related to the dimensions of the living fish, a number of specimens of *C. acus* were measured immediately after being killed in 25% alcohol and again after eighteen months preservation in 70% alcohol. The total length was found to decrease by about 6%, the length of the head by about 1% and its depth by about 2%.

V. SYSTEMATIC ARRANGEMENT

Family Carapidae

(Fierasferidae of older literature and originally united with the Ophidiidae, commonly known as fierasfers, pearl-fish or glass-eels).

Familial characters. Small percomorph fishes with slender, elongate, compressed or cylindrical, scaleless bodies, tapering to an acuminate tail ; head short, usually thickest and deepest part of body ; snout blunt and rounded ; eye large, slightly oval, placed high on side of head ; posterior nostril a crescentic slit just in front of the orbit ; anterior nostril circular, on small papilla at about midlength of snout ; mouth large, usually oblique, lower jaw included within upper ; maxilla reaching to or beyond posterior margin of orbit ; teeth on premaxillae, dentaries, palatines and vomer, those of upper jaw being the smallest and those of the vomer usually the largest ; tongue smooth, pointed, free at tip ; gill-openings wide, the four membranes little united and leaving most of the isthmus uncovered ; branchiostegals 6 or 7 ; top posterior margin of operculum prolonged as small point projecting back above base of pectoral fins ; anus far forward in adult ; median fins long and low, inserted just behind head and continuous round tip of tail ; no caudal fin ; no pelvic fin or girdle ; pectoral girdle always present, but pectoral fin may be reduced or even absent ; sexes not distinguishable on external characters ; eggs pelagic ; life history complex, probably always involving a planktonic larva (vexillifer) and a benthic larva (tenuis).

Key to Genera and Subgenera—Adults only

1	Teeth in bands on jaws and palatines ; maxilla not concealed by skin	2
	Teeth in single rows on jaws and palatines ; maxilla concealed by skin	3
2 (1)	No diastema in lower jaw ; anus almost vertically below base of pectoral	4
	Diastema in lower jaw ; anus clearly posterior to base of pectoral	*Echiodon*
3 (1)	Pectoral fins present	*Encheliophis* (*Jordanicus*)
	Pectoral fins absent	*Encheliophis* (*Encheliophis*)
4 (2)	Anterior teeth not fang-like, body slightly compressed or cylindrical, deepest part usually the head	*Carapus* (*Carapus*)
	Anterior pair of teeth in each jaw large, fang-like ; body strongly compressed, deepest part behind head	*Carapus* (*Onuxodon*)

Genus *CARAPUS* Refinesque 1810

Type *Gymnotus acus* Linnaeus

Carapus Rafinesque-Schmaltz, 1810, *Indice d'Ittiologia Siciliana* : 57. No type stated ; *Gymnotus acus* Linnaeus was designated type by Opinion 42 of the International Commission for Zoological Nomenclature, 1912.

Fierasfer Oken, 1817, *Isis*, 1817 : 1182. Name derived from " les fierasfers ", Cuvier 1815, *Mém. Mus. Hist. nat. Paris*, **1** : 119. Type *Ophidium imberbe* Cuvier, 1815, (non *Ophidion imberbis* Linnaeus, 1758, *Systema Naturae*, **1** : 259).

Diaphasia Lowe, 1843, *Proc. zool. Soc., Lond.* **11** : 92. Type *Gymnotus acus* Brünnich, 1768, *Ichthyologia Massiliensis* : 13.

Oxybeles Richardson, 1844, *Ichthyology of the Voyage of H.M.S. " Erebus " and " Terror "* : 73. Type *Oxybeles Homei* Richardson, 1844.

Porobronchus Kaup, 1860, *Ann. Mag. nat. Hist.* (3) **6** : 272. Type *Porobronchus linearis* Kaup, 1860.

Helminthodes Gill, 1864, *Proc. Acad. nat. Sci. Philadelphia*, **16** : 203 (non *Helminthodes* Marsh, 1864, *Amer. J. Sci.* **38** : 415). Type *Oxybelus lumbricoides* Bleeker, 1854, *Nat. Tijdschr. Ned.-Ind.* **7** : 163.

Vexillifer Gasco, 1870, *Bull. Assoc. Nat. Med. Napoli*, **1870** : 59. Type *Vexillifer dephilippii* Gasco, 1870.

Helminthostoma Cocco. MS name cited by Günther, 1870, *Catalogue of Fishes*, **8** : 145. Type *Helminthostoma delle Chiaje* Cocco.

Lefroyia Jones (J. M.), 1874, *Zoologist*, (2) **9** : 3837. Type *Lefroyia bermudensis* Jones, 1874.

Rhizoiketicus Vaillant, 1893, *C.R. Acad. Sci., Paris*, **117** : 745. Type *Rhizoiketicus carolinensis* Vaillant, 1893.

Leptofierasfer Meek & Hildebrand, 1928, *Publ. Field Mus. zool. Ser.* **15** : 963. Type *Leptofierasfer macrurus* Meek & Hildebrand, 1928.

Pirellinus Whitley, 1928, *Rec. Austral. Mus.* **16** : 211. Type *Oxybeles lumbricoides* Bleeker, 1854.

Disparichthys Herre, 1935, *Publ. Field Mus. zool. Ser.* **18** : 383. Type *Disparichthys fluviatilis* Herre, 1935.

GENERIC CHARACTERS. Body compressed or cylindrical ; lateral processes of first and second vertebrae long and not expanded, of third and fourth vertebrae expanded and fused together, of fifth and subsequent vertebrae short and not expanded ; trunk vertebrae number 17–20 ; lower jaw stout, nearly straight, tooth-bearing portion tapering to tip ; in adult, teeth of jaws and palatines arranged in bands ; distance between teeth approximately equal to diameter of tooth-base ; no diastema in lower jaw ; maxilla extending beyond posterior edge of orbit in adult, clearly outlined by folds of skin ; interorbital domed ; upper edge of orbit not impinging on dorsal profile of head ; anus in adult close to roots of pectoral fins ; swim-bladder short ; no pyloric caecae ; branchiostegals 7.

The most familiar name for members of the Carapidae is " fierasfer ", a term first used by Brünnich (1768) who gave it as a local name for the species now known as *Carapus acus* in use by the fishermen of Marseilles. The name next appears as " les fierasfers " (Cuvier, 1815 and 1817) when it was used for a group of subgeneric rank under *Ophidium*, containing *Ophidium imberbe* (a synonym of *Carapus acus*) and *Ophidium dentatum* (now *Echiodon dentatus*). This was quickly given nomenclatural status as *Fierasfer* Oken (1817), the name which has been and is still the most widely used for members of this family.

However prior to Cuvier, the heterogenous Linnean genus *Gymnotus* had been divided into *Gymnotus, sensu strictu,* and *Carapus* by Rafinesque-Schmaltz (1810). Rafinesque did not specify a type for the new genus, nor even list the species it was created to contain, but gave only the following diagnosis :—

> " XII. Nessun'ala dorsale, ne caudale, un'ala anale e due pettorali, mascella superiore più lunga dall'inferiore, coda nuda al disotto. *Osserv.* Differisce dal vero genere *Gymnotus,* che ha l'ala anale lunghissima, ricuoprendo il disotto della coda, e la mascella inferiore più lunga dalla superiore." (XII. Neither dorsal nor caudal fins ; an anal fin and two pectorals ; upper jaw longer than the lower ; tail naked below. *Notes.* It differs from the true genus *Gymnotus,* which has the anal fin very long, covering the lower part of the tail, and the lower jaw longer than the upper.)

In another part of his account, Rafinesque cited *Gymnotus acus* Linnaeus as a Sicilian representative of *Carapus.* By Opinion 42, rendered 1912, the International Commission for Zoological Nomenclature has designated *Gymnotus acus* Linnaeus (no date given) as type of *Carapus* Rafinesque, invalidating *Fierasfer* as a generic name.

Gymnotus acus Linnaeus does not, strictly, exist at all and the characters used by Rafinesque in his diagnosis of *Carapus* are such as to exclude from this genus all species of fierasfer. Rafinesque derived his nomenclature from the 13th edition of the *Systema Naturae,* edited by Gmelin (1788), in which is a shortened description of *Gymnotus acus* Brünnich, correctly attributed, the species that Rafinesque presumably intended to name. The diagnosis of *Carapus* is apparently a translation into Italian of Gmelin's Latin description of the South American fresh-water fish *Gymnotus carapo* Linnaeus, type species of the genus *Gymnotus* Linnaeus. The resemblance of the new generic name to the older trivial name emphasizes the similarity of the descriptions.

Of the remaining generic synonyms, *Diaphasia* Lowe was proposed as an alternative to the then current name *Fierasfer.* The species described by Richardson and Jones are so closely akin to *Carapus acus* that generic separation of either is unwarranted, while *Rhizoiketicus* Vaillant must be united with *Carapus* for lack of distinguishing characters. This genus was created to contain a fierasfer from the Caroline Islands, the two examples of which were described as having large, easily-detachable, lozenge-shaped scales above and below the lateral line. These were not true scales, but were formed from and continuous with the outer cornified layers of the skin. Desiccation of any long-preserved fierasfer will cause cracking and flaking of the skin and these " scales " are thus no adequate reason for retaining *Rhizoiketicus* as a separate genus. The other characters of the two specimens are not recorded and they seem to be no longer in existence, nor has the species been found since. The other generic synonyms are based upon larvae. *Porobronchus* Kaup and *Vexillifer* Gasco belong to *C. acus, Helminthodes* Gill, and its substitute *Pirellinus* Whitley, probably to *C. homei,* and *Leptofierasfer* Meek & Hildebrand probably to *C. dubius* ; it seems likely that *Disparichthys* Herre may ultimately also be found to be attributable to a species of *Carapus.*

Recently, *Carapus parvibrachium* Fowler has been made the type of a new genus, *Onuxodon* Smith, 1955, on the grounds that it differs from all other fierasfers in possessing an extremely deep, strongly compressed body, strongly domed interorbital and fewer vertebrae. To these characters may be added a partly calcified swim-bladder and a slightly greater number of trunk vertebrae than occurs in most species of *Carapus*. In all these features the species originally described as *Fierasfer margaritiferae* Rendahl agrees with *C. parvibrachium* and there can be no doubt that the two are congeneric. However, in other respects—vertebral and jaw structure, position of the anus, dentition, general body proportions—these two species are more closely akin to *Carapus* spp. than to the other fierasfers and for this reason it is considered that their probable evolutionary relationships are more truly expressed by regarding *C. parvibrachium* and *F. margaritiferae* as representing a subgenus of *Carapus*. In the following account, therefore, the genus is divided into two subgenera, *Carapus* and *Onuxodon*. It is not improbable that future investigations will result in the creation of a third subgenus to contain *Carapus parvipinnis* (Kaup), but this course is not at present justified.

Subgenus ***CARAPUS***

SUBGENERIC CHARACTERS. Body slightly compressed or cylindrical, not so deep as length of head; interorbital flat or only slightly domed, its width equal to or greater than horizontal diameter of eye; trunk vertebrae 17–18; swim-bladder uncalcified.

KEY TO SPECIES—ADULTS ONLY

1	Head more than one-ninth of total length; pectoral fins more than one-third length of head	2
	Head less than one-ninth of total length; pectoral fins less than one-third length of head	*C. parvipinnis* *C. boraborensis*
2 (1)	No enlarged teeth at front of jaws	6
	Enlarged teeth at front of upper jaw	3
	Enlarged teeth at front of upper and lower jaws	9
3 (2)	Median row of large teeth on vomer, flanked by small teeth	4
	Anterior vomerine teeth small; posterior vomerine teeth large . .	*C. birpex*
4 (3)	Teeth of upper jaw uniserial	*C. pindae*
	Teeth of upper jaw polyserial	5
5 (4)	Outermost series of teeth in lower jaw considerably larger than inner series .	*C. homei*
	Outermost series of teeth in lower jaw not conspicuously larger than inner series	*C. dubius* *C. bermudensis*
6 (2)	Maximum depth of body considerably greater than maximum depth of head .	8
	Maximum depth of body not greater than maximum depth of head . . .	7
7 (6)	Anus anterior to roots of pectoral fins	*C. acus*
	Anus vertically beneath roots of pectoral fins	*C. kagoshimanus*
8 (6)	Pectoral one-third length of head; body progressively tapering from region of maximum depth to tip of tail	*C. houlti*
	Pectoral more than one-half length of head; body narrowing sharply at end of abdomen before tapering to tail tip	*C. cuspis*
9 (2)	Head one-eighth to one-ninth of total length (about 200 mm.); outer series of teeth in lower jaw similar to inner series	*C. owasianus*
	Head one-sixth to one-seventh of total length (about 100 mm.); outer series of teeth in lower jaw much taller than inner series	*C. caninus*

Carapus acus (Brünnich), 1768

(Text-fig. 6)

Gymnotus acus Brünnich, 1768, *Ichthyologia Massiliensis* : 13. Artedi, 1788, *Bibliotheca Ichthyologica* : 164. Gmelin, 1788, *Systema Naturae Linnaei*, **1** : 1140.

Notopterus Fontanesii Risso, 1810, *Ichthyologie de Nice* : 82.

Ophidium imberbe Cuvier, 1815, *Mém. Mus. Hist. Nat., Paris*, **1** : 119. (non *Ophidion imberbis* Linnaeus, 1758, *Systema Naturae*, **1** : 259.) Cuvier, 1817, *Règne Animal*, **2** : 259.

Fierasfer imberbe, Oken, 1817, *Isis*, **1817** : 1182.

Ophidium fierasfer Risso, 1826, *Histoire Naturelle des Principales Productions de l'Europe Méridionale*, **3** : 212.

Fierasfer fontanesii, Costa (O.), 1829, *Fauna del Regno di Napoli*, **3** : tab. 20 bis.

Ophidium sp., Delle Chiaje, 1841, *Descrizione e Notomia degli Animali Invertebrati della Sicilia Citeriore*, **4** : 3.

Diaphasia acus, Lowe, 1843, *Proc. zool. Soc., Lond.* **11** : 92.

Fierasfer acus, Kaup, 1856, *Arch. Naturges.* **22** : 93. Kaup, 1856, *Catalogue of Apodal Fish* : 157. Günther, 1862, *Catalogue of Fishes*, **4** : 381. Steindachner, 1868, *S.B. Akad. Wiss. Wien*, **57** : 46. Canestrini, 1872, *Fauna d'Italia :* Pesci : 191. Emery, 1878, *Atti. Soc. ital. Sci. nat., Milano*, **21** : 37. Emery, 1880, *Fauna u. Flora Neapel*, **2** : 1. Giglioli, 1880, *Esposizione di Pesca* : 97. Perugia, 1881, *Elenco dei Pesci dell'Adriatica* : 38. Emery, 1882, *Mitt. zool. Stat. Neapel*, **3** : 281. Carus, 1885, *Prodromus Faunae Mediterranae*, **2** : 580. Raffaele, 1888, *Mitt. zool. Stat. Neapel*, **8** : 39. Lo Bianco, 1904, *Pelagische Tiefseefischerei der Maja in der Umbegung von Capri* : 24. Šoljan, 1948, *Ribe Jadrana* : 122.

Helminthostoma delle Chiaje Cocco. MS name cited by Günther, 1870, *Catalogue of Fishes*, **8** : 145.

Fierasfer massiliensis Brünnich. Name cited by Kaup, 1856, *Catalogue of Apodal Fish* : 157, without reference.

Porobronchus linearis Kaup, 1860, *Ann. Mag. nat. Hist.* (3) **6** : 272. Günther, 1870, *Catalogue of Fishes*, **9** : 145. Belotti, 1891, *Atti Soc. ital. Sic. nat., Milano*, **33** : 127.

Vexillifer dephilippii Gasco, 1870, *Bull. Assoc. Nat. Med., Napoli*, **1870** : 59.

Vexillifer de Filippii, Costa (A.), 1871, *Ann. Mus. zool., Napoli*, **6** : 88.

Encheliophis tenuis Putnam, 1874, *Proc. Boston Soc., nat. Hist.* **16** : 343.

Fierasfer dentatus (part), Emery, 1880, *Fauna u. Flora Neapel*, **2** : 16.

Fierasfer dentatus, Emery, 1882, *Mitt. zool. Stat. Neapel*, **3** : 283.

Fierasfer imberbis, Moreau, 1881, *Histoire Naturelle des Poissons de la France*, **3** : 226. Moreau, 1892, *Manuel d'Ichthyologie Française* : 405.

Carapus imberbis, Fowler, 1936, *Bull. Amer. Mus. nat. Hist.* **70** : 1073.

Carapus acus, Padoa, 1947, *Pubbl. Staz. zool. Napoli*, **20** : 111. Arnold, 1953, *Pubbl. Staz. zool. Napoli*, **24** : 153.

The material examined includes 39 specimens in the collection of the British Museum (Natural History) ; 17 in the collection of the Institut Océanographique de Monaco ; 22 in the collection of the Universitetets Zoologiske Museum, Copenhagen ; 40 in the Naples Sales Collection, 1952 ; and 29 in the Naples Sales Collection, 1954. Of these 147 specimens the majority were adults or juveniles, only a few being vexillifer or tenuis larvae. The localities represented were Sicily, Naples, Genoa, Monaco and Nice. The type, which was obtained at Marseilles, France, may be no longer in existence.

SPECIFIC CHARACTERS. *Adult* : Maximum length about 200 mm. ; length of head one-seventh to one-eighth of total length ; maximum depth of head one-half and maximum width one-third of length of head ; horizontal diameter of eye equal to length of snout and to interorbital width ; mouth very oblique ; maxilla extends only a short distance posterior to orbit ; jaw teeth small and uniform ; vomerine teeth a little longer than jaw teeth, arranged in three slightly irregular, longitudinal rows, those of the central row being the largest ; pectoral fins one-half length of head ; anus anterior to roots of pectorals ; body slightly translucent in life, heavily blotched or barred with red ; about fifteen golden or silvery spots along flanks just above lateral line ; iris silver ; operculum and abdomen often with silvery lustre.

Juvenile : Adult colouration first assumed at about 100 mm. length ; general body form resembles that of adult, though head of younger individuals may be but one-ninth or one-tenth of total length ; dentition and proportions of head similar to those of adult ; maxilla extends little beyond hind edge of orbit ; pectorals one-third or less of length of head ; anus beneath or slightly anterior to roots of pectorals ; body translucent, spotted or barred with dark-brown or black ; no sign of red pigment whatsoever ; golden or silvery spots along sides as in adult.

Tenuis larva : Maximum recorded length more than 200 mm.; body slender and cylindrical, not compressed as in juvenile and adult ; head less than one-twelfth of total length ; maxilla extends only as far as middle of orbit ; teeth in single rows on jaws and palatines ; enlarged teeth may be present at front of one or both jaws ; pectoral fins less than one-fifth length of head ; anus posterior to roots of pectorals ; transparent and unpigmented in life.

Vexillifer larva : Maximum recorded length more than 80 mm.; head about one-tenth of total length ; maxilla extends only to anterior edge of orbit ; teeth in single rows on jaws and palatines ; older vexillifers have enlarged teeth at front of one or both jaws ; pectoral fins about one-eighth of length of head ; anus near posterior end of abdomen ; body translucent in life and devoid of pigmentation.

Eggs : Spawning period July-September ; eggs adhere in oval, yellowish rafts about 80 mm. in length.

The main dimensions of the adult fish studied are summarized in Table I and measurements and proportions of representative specimens are given in Table II.

TABLE I.—Carapus acus (*Brünnich,*) 1768. *Summary of Measurements and Proportions of Adults.*

Variate.	N.	R. mm.	M ± σ_M. mm.
Total length	72	100–202	155·4±2·34
Length of head	73	13–28	20·6±1·08
Depth of head	72	7–16	11·3±0·23
Width of head	49	4–11	8·0±0·25
Length of pectoral	49	7–16	10·6±0·30
Preanal length	49	13–23	18·7±0·37
		%	%
Length of head (% TL)	72	11·6–15·3	13·2±0·08
Depth of head (% HL)	72	43·8–71·4	55·0±0·69
Width of head (% HL)	53	26·7–50·0	38·6±0·23
Length of pectoral (% HL)	48	38·8–64·0	51·6±0·84
Preanal length (% TL)	47	10·8–13·3	11·6±0·10

N = number of specimens ; R = range of variate ; M = mean of variate (± standard error of mean, σ_M) ; TL = total length ; HL = length of head.

TABLE II.—Carapus acus (*Brünnich*), 1768. *Measurements and proportions of representative adults.*

Collection	British Museum	
Museum number	1952.11.25.1	1952.11.25.5
Locality	Naples	
	mm.	mm.
Total length	184	152
Length of head	24 (13% TL)	20 (13% TL)
Maximum depth of head	14 (58% HL)	11 (55% HL)
Maximum width of head	10 (42% HL)	9 (45% HL)
Length of snout	4 (17% HL)	3·5 (17·5% HL)
Horizontal diameter of eye	4 (17% HL)	3·5 (17·5% HL)
Verical diameter of eye	3·5 (15% HL)	3·2 (16% HL)
Interorbital width	4 (17% HL)	4 (20% HL)
Length of maxilla	11 (46% HL)	9·5 (47·5% HL)
Length of pectoral fin	12 (50% HL)	10 (50% HL)
Preanal length	22 (12% TL)	18 (12% TL)
Maximum depth of body	14·5 (60% HL)	13·5 (67·5% HL)

TL = total length ; HL = length of head.

C. acus is quite common in the western Mediterranean, being recorded from the coastal waters of Spain, France, Italy, Sicily, Sardinia and the Balearic Islands. It may also occur in the Adriatic, Aegean and off the Algerian coast and has occasionally been reported in the Atlantic. These latter records, however, are of doubtful validity. *C. acus* has occasionally been taken free-swimming, but all stages except the vexillifer normally live within the body cavities of holothurians (*Holothuria tubulosa* and *Stichopus regalis*), where they attack the gonads and branchial trees. The tenuis larva is entirely dependent upon its host and does not survive long in sea water.

Carapus birpex n. sp.

(Text-fig. 7)

The type, the only specimen known, is an adult, found in a holothurian taken at Madeira, precise locality unknown. It is in the collection of the Museu Municipal, Funchal, Madeira, museum no. 2739. Two other fierasfers were found in the same holothurian, but it is unknown whether they have been preserved.

SPECIFIC CHARACTERS. Length of type 209 mm. ; head one-seventh of total length ; maximum depth of head more than three-fifths and maximum width one-fifth of length of head ; horizontal diameter of eye equal to length of snout and slightly less than interorbital width ; mouth very oblique ; maxilla extends behind orbit for distance equal to half horizontal diameter of eye ; owing to obliquity of mouth, end of maxilla almost cuts ventral profile of lower jaw ; single pair of enlarged teeth at front of upper jaw, the rest, like those of the lower jaw, small and uniform ; anterior half of vomer bears two slightly irregular rows of small, sharp, conical teeth, at either side of which the antero-lateral surfaces of vomer are smooth and toothless ; posterior portion of vomer has a single median row of five, large, stout,

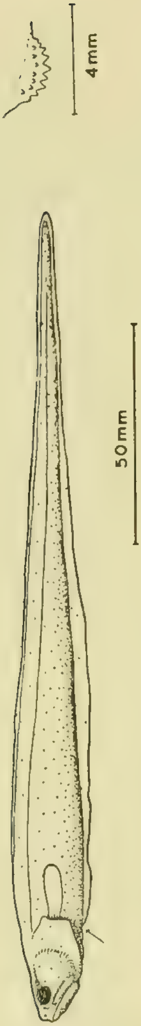


Fig. 6.—*Carapus acus* (Brünnich). A representative adult and its vomerine teeth.

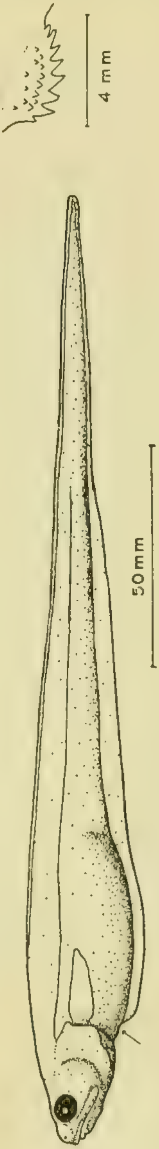


Fig. 7.—*Carapus cuspis* n. sp. Type, and vomerine teeth.

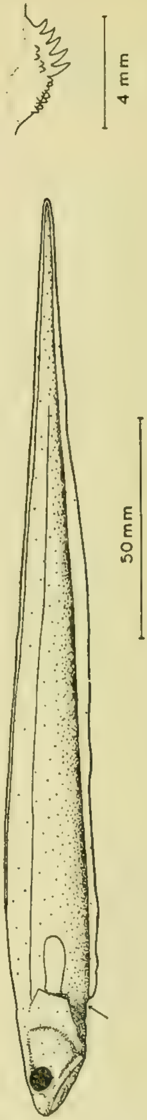


Fig. 8.—*Carapus birpex* n. sp. Type, and its vomerine teeth.

curved and sharply-pointed teeth, flanked by a number of smaller teeth similar to those on front of vomer; pectoral fins about two-fifths length of head; anus anterior to roots of pectorals; colour in life unknown. The other stages in the life history are unidentified.

The dimensions of the type are given in Table III.

TABLE III.—Carapus birpex *n. sp. Measurements and Proportions of the Type.*

Museum . . . . Museu Municipal, Funchal.
Locality . . . . Madeira.

	mm.	
Total length	209	
Length of head	29	(14% TL)
Maximum depth of head	15·5	(58% HL)
Maximum width of head	11	(39% HL)
Length of snout	5·5	(19% HL)
Horizontal diameter of eye	5·5	(19% HL)
Vertical diameter of eye	5	(17% HL)
Interorbital width	6	(21% HL)
Length of maxilla	15	(52% HL)
Length of pectoral fin	12	(41% HL)
Maximum depth of body	18	(62% HL)
Preanal length	25	(12% TL)

TL = total length; HL = length of head.

Carapus cuspis n. sp.

(Text-fig. 8)

The three known examples of this species were taken free-swimming near Madeira, position 33° 02′ N., 16° 20′ W., depth 100 metres (about 50 fathoms), during the 1897 cruise of the yacht " Princesse-Alice ". They were recorded, without description or figure, as *Fierasfer acus* by Roule (1917). The smallest of the three specimens is designated type and this and one paratype are in the collection of the Institut Océanographique de Monaco. A second paratype is in the collection of the British Museum (Natural History).

SPECIFIC CHARACTERS. Length of type 216 mm. (of paratypes 221 mm. and 230 mm.); head a little more than one-eighth of total length; maximum depth of head two-thirds and maximum width one-half of length of head; horizontal diameter of eye slightly greater than length of snout, but less than interorbital width; mouth oblique; maxilla extends behind orbit for distance equal to half horizontal diameter of eye; teeth on jaws and palatines resemble those of *C. acus*; vomer with single row of rather large, sharp, backwardly-directed teeth, flanked by a few smaller ones; anal fin deep, fleshy anteriorly; pectorals three-fifths length of head; anus slightly anterior to roots of pectoral fins. Colour in life unknown. Other stages in the life history have not been identified.

The body does not taper steadily from head to tail-tip, as in most fierasfers. Instead, the abdomen is deep and rounded and the maximum depth of the body is about 40% greater than the maximum depth of the head. Beyond the abdomen the body narrows sharply to the long, tapering tail.

The paratypes closely resemble the type, differing only in their dimensions and in some minor details of their proportions. Through long preservation in alcohol their colour has been entirely destroyed, but a record from Algiers (Guichenot, 1850) may perhaps refer to this species. In this account a fierasfer, said to be common along the Algerian coast, was identified as *Fierasfer imberbe* and described as having a yellowish ground colour crossed by numerous brown bands, the abdomen bluish and faintly spotted with red. This colour scheme is quite unlike that characteristic of *C. acus*.

The dimensions of the type and paratypes of *C. cuspis* are given in Table IV.

TABLE IV.—Carapus cuspis *n. sp. Measurements and Proportions of Type and Two Paratypes.*

Collection	Monaco		Monaco		British Museum.	
Status	Type		Paratypes 1 and 2			
	mm.		mm.		mm.	
Total length	216		221		230	
Length of head	28	(13·0% TL)	30	(13·6% TL)	31	(13·5% TL)
Maximum depth of head	17	(61% HL)	17	(57% HL)	18	(58% HL)
Maximum width of head	13	(46% HL)	13	(43% HL)	14	(45% HL)
Length of snout	5	(18% HL)	5	(17% HL)	5	(16% HL)
Horizontal diameter of eye	6	(21% HL)	6	(20% HL)	6	(19% HL)
Vertical diameter of eye	5	(18% HL)	5	(17% HL)	5	(16% HL)
Interorbital width	6·5	(23% HL)	6·5	(22% HL)	7	(23% HL)
Length of maxilla	15	(54% HL)	15	(50% HL)	17	(55% HL)
Maximum depth of body	24	(86% HL)	24	(80% HL)	22	(71% HL)
Length of pectoral fin	17	(61% HL)	17	(57% HL)	17	(65% HL)
Preanal length	27	(2·5% TL)	27	(13% TL)	28	(12% TL)

TL = total length ; HL = length of head.

The two new species, *C. birpex* and *C. cuspis*, are both from the same general locality and both bear a superficial resemblance to *C. acus*, to which species they are probably most closely related. They differ from it and from each other especially in their dentition, the size and form of their maxillae and the general shape and proportions of the head, as well as in absolute size. Of the two, *C. birpex* is the furthest removed from *C. acus*. The snout is considerably more pointed than is that of *C. acus* when viewed from the side, squarer when viewed from above (Text-fig. 9). Further, though the head of *C. birpex* is longer than that of the largest *C. acus* available for study, yet the snout is of no greater length. Hence the preorbital portion of the skull is relatively shorter in *C. birpex*, the postorbital relatively longer. Another important difference between the two species is the obliquity of the mouth, which in *C. birpex* is so great that the maxilla almost impinges on the ventral profile of the lower jaw, though it does not in fact extend so far behind the orbit as does the maxilla of *C. acus*. Finally, *C. birpex* is separated from *C. acus* by the possession of enlarged teeth at the front of the upper jaw and by the dual nature of the vomerine teeth, which in form and arrangement are quite unlike those of any other species of *Carapus* so far described. *C. birpex* resembles the Indo-Pacific species *C. homei* in having enlarged jaw teeth, but differs from this species in the absence of an outer row of strong teeth in the lower jaw.

C. cuspis, on the other hand, resembles *C. acus* in many respects, particularly in the dentition of the jaws and the proportions of the head. But the maxilla is relatively shorter than is that of *C. acus*, though the obliquity of the mouth is no greater, and the median row of vomerine teeth are larger and more strongly curved. *C. cuspis* is most clearly distinguished by the depth and rotundity of the abdomen and especially by the constriction of the body at the base of the tail.

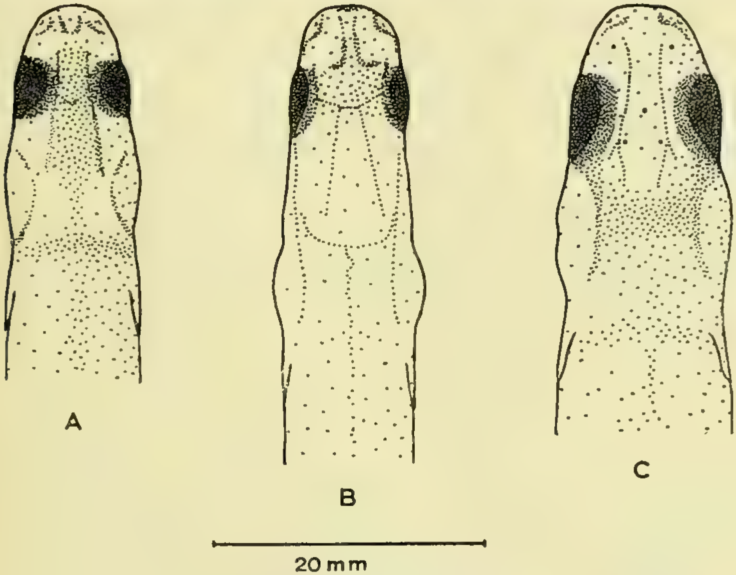


FIG. 9.—Heads of European *Carapus* spp. from the dorsal aspect.
A. *C. acus*; B, *C. birpex*; C, *C. cuspis*.

C. acus has been recorded from Atlantic localities upon a number of occasions and under a variety of names:

Madeira, as *Diaphasia acus* (Lowe, 1843).
Canary Islands, as *Fierasfer acus* (Vinciguerra, 1893).
Portuguese coast, as *Fierasfer imberbis* (Nobre, 1935).
Portuguese coast, as *Carapus imberbis* (de Buen, 1935).
West Africa, as *Carapus imberbis* (Fowler, 1936).
Cape Verde Islands, as *Carapus imberbis* (Cadenat, 1937).
Biarritz, as *Fierasfer imberbis* (Pellegrin, 1937).
Senegal, as *Carapus imberbis* (Cadenat, 1950).

Of these authors, two alone (Nobre, 1935; Fowler, 1936) provided a description, both of which were based upon Mediterranean specimens, not on those from the locality at which the species was reported. Nobre included a figure, but this is unrecognizable. It seems probable that these records relate either to *C. birpex* or to *C. cuspis*, not to *C. acus* at all.

Carapus dubius (Putnam), 1874

(Text-fig. 10A)

Fierasfer dubius (part) Putnam, 1874, *Proc. Boston Soc. nat. Hist.* **16** : 339. Jordan & Gilbert, 1882, *Bull. U.S. nat. Mus.* **16** : 791.
Fierasfer arenicola Jordan & Gilbert, 1881, *Proc. U.S. nat. Mus.*, **4** : 338. Jordan, 1895, *Proc. Calif. Acad. Sci.* (2) **5** : 502. Jordan & Evermann, 1898, *Bull. U.S. nat. Mus.* **47** : 2183.
Fierasfer affinis, Jordan & Evermann, 1898, *Bull. U.S. nat. Mus.*, **47** : 2183. (non Günther, 1862, *Catalogue of Fishes*, **4** : 381.)
Carapus dubius, Meek & Hildebrand, 1928, *Publ. Field Mus. zool. Ser.* **15** : 963.
Leptofierasfer macrurus Meek & Hildebrand, 1928, *Publ. Field Mus. zool. Ser.* **15** : 963.
Carapus affinis (part), Rivero, 1936, *Proc. Boston Soc. nat. Hist.* **41** : 41. (non Günther, 1862.)

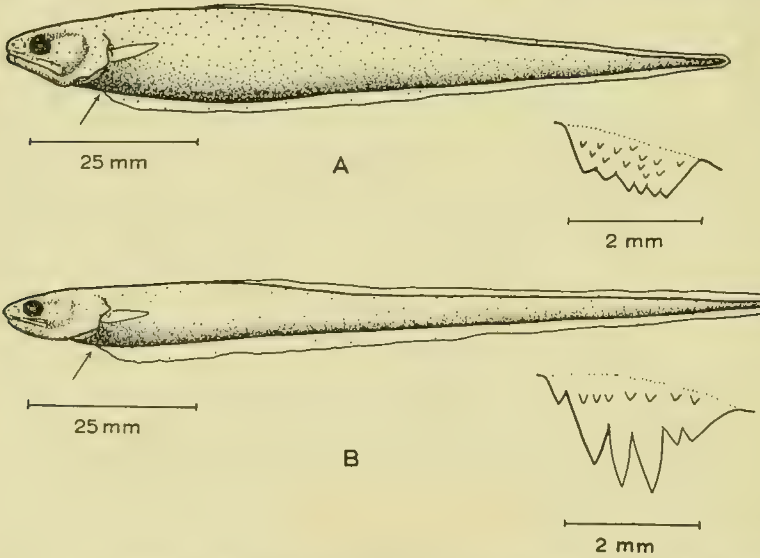


Fig. 10.—A, *Carapus dubius* (Putnam), and its vomerine teeth. B, *Carapus bermudensis* (Jones), and its vomerine teeth.

The following account is based upon a single adult in the collection of the British Museum (Natural History) from the Gulf of Panama.

Putnam did not designate a type. His description was based upon fourteen specimens, eight from Pearl Island, in the Gulf of Panama, the rest from Florida, the Bahamas and the Tortugas. Most of these specimens, including five from Panama, are in the Museum of Comparative Zoology, Harvard. In Putnam's list of specimens those from Pearl Island stand first; they must therefore be regarded as the cotypes and Pearl Island, Gulf of Panama, as the type locality.

SPECIFIC CHARACTERS. Maximum length apparently about 100 mm.; head one-seventh to one-eighth of total length; maximum depth of head one-half to three-fifths and maximum width one-third to two-fifths of length of head; horizontal diameter of eye equal to length of snout, greater than interorbital width; mouth slightly oblique; maxilla extending only a short distance behind posterior edge of orbit; teeth of upper jaw small, one or two anterior ones enlarged; outermost series of lower jaw slightly stouter than inner series; row of about four large, stout, conical teeth on vomer, flanked by smaller ones; pectoral fin three-fifths length of head; anus anterior to roots of pectorals; translucent in life, a few yellowish spots on sides of body, tip of tail dusky (Jordan & Gilbert, 1881). Vexillifer larvae attributable to this species have been described under the name *Leptofierasfer macrurus* Meek & Hildebrand (1928).

The measurements and proportions of the only specimen available for study are given in Table V.

TABLE V.—Carapus dubius (*Putnam*), 1874, *and* C. bermudensis (*Jones*), 1874. *Measurements and Proportions of Adult Specimens.*

Collection	British Museum			
Species	*C. dubius*		*C. bermudensis*	
Museum number	1935.3.24.26		1931.9.24.1	
Locality	Gulf of Panama		Florida	
	mm.		mm.	
Total length	108		104	
Length of head	16	(15% TL)	15	(14% TL)
Maximum depth of head	10	(62·5% HL)	7	(47% HL)
Maximum width of head	7	(44% HL)	5	(33% HL)
Length of snout	3·5	(22% HL)	2·5	(17% HL)
Horizontal diameter of eye	3·5	(22% HL)	2·5	(17% HL)
Vertical diameter of eye	3·2	(20% HL)	2	(13% HL)
Interorbital width	3	(19% HL)	3	(20% HL)
Length of maxilla	8	(50% HL)	6·5	(43% HL)
Length of pectoral fin	10	(62·5% HL)	7	(47% HL)
Maximum depth of body	11	(69% HL)	7·5	(50% HL)
Preanal length	14	(13% TL)	12	(12% TL)

TL = total length; HL = length of head.

C. dubius has been recorded from the Pacific coast of Central America, including Pearl Island and Chame Point, Gulf of Panama; Mazatlan, Mexico; and the Gulf of California. Examples have been found lying free in the sand, but the majority of specimens have been taken as inquilines of lamellibranchs.

The taxonomic status of the fierasfers from the Pacific and Atlantic sides of Central America is a matter concerning which, through lack of specimens, no final decision can yet be made. In 1874, two species, both undoubted *Carapus*, were described—*Lefroyia bermudensis* Jones from Bermuda and *Fierasfer dubius* Putnam from the Gulf of Panama and West Indies. Neither was figured, the type of *L. bermudensis* cannot be traced, and the original descriptions are distinguishable neither from each other nor from that of the Indo-Pacific species *C. homei*. Most authors have regarded *C. dubius* and *C. bermudensis* as conspecific and many have further equated them with *Fierasfer affinis* Günther. Further complications were introduced by the designation of *Fierasfer arenicola* Jordan & Gilbert and *Leptofierasfer macrurus* Meek & Hildebrand, a vexillifer larva. *Fierasfer arenicola* is now generally accepted as a synonym of *F. dubius*, and the larval nature of *L. macrurus* has also been recognized (Parr, 1930).

Now, it is quite clear that all these forms, whatever their status, belong to the one genus *Carapus*. Further, there is no reason for uniting *F. affinis*, the locality of which is unknown, with the American fierasfers. This species, the type of which is in the British Museum, is far larger than any described from American water and (p. 277) is not distinguishable from *C. homei*.

Putnam based his description of *F. dubius* upon specimens from the Gulf of Panama, but was unable to distinguish them from others from the West Indies. The identity of the two forms is supported by Rivero (1936) who re-examined such of Putnam's specimens as are still available and compared them with other material from Cuba and Jamaica. It appears best, however, to consider these Pacific and Atlantic fierasfers as two closely-related species, pending re-examination of the problem on the basis of more adequate material. The trivial name *dubius* should be restricted to the Pacific fierasfers, while the trivial name *bermudensis* is available for those from the Atlantic.

Carapus bermudensis (Jones), 1874

(Text-fig. 10B)

Lefroyia bermudensis Jones (J. M.), 1874, *Zoologist* (2) **9** : 3837.

Fierasfer dubius (part), Putnam, 1874, *Proc. Boston Soc. Nat. Hist.* **16** : 343. Jordan & Gilbert, 1882, *Bull. U.S. nat. Mus.* **16** : 791.

Fierasfer bermudensis, Jordan & Evermann, 1898, *Bull. U.S. nat. Mus.*, **47** : 2443. Herre, 1942, *Stanford Univ. Publ. biol. Sci.* **7** (2) : 20.

Fierasfer dubius, Parker, 1926, *Proc. nat. Acad. Sci. Washington*, **12** : 421.

Carapus dubius (part), Meek & Hildebrand, 1928, *Publ. Field Mus. zool. Ser.* **15** : 963.

Fierasfer affinis, Breder, 1929, *Field Book of Marine Fishes of the Atlantic Coast* : 279. (non Günther, 1862.)

Carapus affinis, Rivero, 1936, *Proc. Boston. Soc. nat. Hist.* **41** : 41. (non Günther, 1862.)

Carapus sp., juv., Parr, 1930, *Bull. Bingham Oceanogr. Coll.* **3** : 133.

Carapus bermudensis, Longley & Hildebrand, 1941, *Papers Tortugas Lab.* **34** : 90. Beebe & Tee-Van, 1933, *Field Book of the Shore Fishes of Bermuda* : 232.

Fierasfer sp., larva, Herre, 1942, *Stanford Univ. Publ. biol. Sci.* **7** (2) : 20.

The specimens examined are five adults and six larvae in the collection of the British Museum (Natural History). The localities represented are (adults) Florida, Cayman Islands, St. Kitts, Antigua, (larvae) Grenada, Tobago, Antigua. The type was obtained at Bermuda, but is probably no longer in existence.

Specific characters. Maximum length probably less than 150 mm; head one-seventh to one-eighth of total length; maximum depth of head one-half and maximum width two-fifths of length of head; horizontal diameter of eye greater than length of snout and interorbital width; mouth oblique; maxilla not extending far behind posterior edge of orbit; outermost teeth of lower jaw slightly larger than those of inner series; two to four large conical teeth on vomer, flanked by smaller teeth; in upper jaw, anterior teeth enlarged; according to Rivero (1936) there is a single row of small, sharp, backwardly-directed teeth along the outer side of the premaxilla, hidden by the lips, but these are not present in all specimens; pectoral fins two-fifths to one-half length of head; anus anterior to roots of pectoral fins; translucent in life, with irregular transverse reddish bands on trunk and silvery bar along sides (Longley & Hildebrand, 1941). There is a vexillifer larva attributable to this species.

Measurements and proportions of a representative specimen are given in Table V.

C. bermudensis occurs in the west central Atlantic area, including Bermuda, Florida, the Bahamas, Cuba, Jamaica, Cayman Islands, Haiti, Leeward Islands, Windward Islands, Trinidad and Tobago. It is inquiline in the holothurian *Actinopyga agassizi.*

Carapus homei (Richardson), 1844

(Text-fig. 11)

Oxybeles Homei Richardson, 1844, *Ichthyology of the Voyage of H.M.S. Erebus and Terror*: 73. Bleeker, 1855, *Verh. Akad. Amsterdam*, **2**: 15.

Oxybelus Brandesii Bleeker, 1851, *Nat. Tijdschr. Ned.-Ind.* **1**: 278. Bleeker, 1851, *Nat. Tijdschr. Ned.-Ind.* **2**: 228. Bleeker, 1852, *Nat. Tijdschr. Ned.-Ind.* **3**: 238. Bleeker, 1852, *Verh. Bat. Gen.* **24**: 24. Bleeker, 1854, *Nat. Tijdschr. Ned.-Ind.* **7**: 162. Bleeker, 1854, *Nat. Tijdschr. Ned.-Ind.* **7**: 495. Bleeker, 1858, *Nat. Tijdschr. Ned.-Ind.* **15**: 255.

? *Oxybelus lumbricoides* Bleeker, 1854, *Nat. Tijdschr. Ned.-Ind.* **7**: 163.

Fierasfer neglectus Peters, 1855, *Arch. Naturges.* **21**: 260. Günther, 1862, *Catalogue of Fishes*, **4**: 381. Regan, 1908, *Trans. linn. Soc. Lond.* **12**: 220. Barnard, 1927, *Ann. S. Afr. Mus.* **21**: 884.

Fierasfer Homei, Kaup, 1856, *Catalogue of Apodal Fish*: 157. Putnam, 1874, *Proc. Boston Soc. nat. Hist.* **16**: 343. Bleeker, 1863, *Ned. Tijdschr. Dierk.* **1**: 236. Bleeker, 1863, *Ned. Tijdschr. Dierk.* **1**: 272. Bleeker, 1865, *Ned. Tijdschr. Dierk.* **2**: 293. Alleyne & Macleay, 1876, *Proc. linn. Soc., N.S.W.* **1**: 347.

Fierasfer Brandesii, Bleeker, 1858, *Nat. Tijdschr., Ned.-Ind.* **15**: 204. Bleeker, 1858, *Nat. Tijdschr. Ned.-Ind.* **15**: 461.

Fierasfer homei, Günther, 1862, *Catalogue of Fishes*, **4**: 381. Day, 1889, *The Fauna of British India, Fishes*, **2**: 436. Fowler, 1900, *Proc. Acad. nat. Sci. Philadelphia*, **1900**: 523. Johnstone, 1904, *Ceylon Pearl Oyster Fisheries*, 1904, *Suppl. Rep. no.* 15: 211. Jordan & Everman, 1903, *Bull. U.S. Fish Comm.* **23**: 505. Jordan & Seale, 1905, *Bull. Bur. Fish.* **25**: 435. Jordan & Seale, 1906, *Bull. Bur. Fish.* **26**: 48. Jordan & Snyder, 1906, *Bull. Bur. Fish.* **26**: 217. Regan, 1908, *Trans. linn. Soc. Lond.* **12**: 220.

Fierasfer affinis Günther, 1862, *Catalogue of Fishes*, **4**: 381.

? *Fierasfer lumbricoides*, Bleeker, 1865, *Ned. Tijdschr. Dierk.* **2**: 192. Regan, 1908, *Trans. linn. Soc. Lond.* **12**: 220.

? *Helminthodes lumbricoides*, Gill, 1864, *Proc. Acad. nat. Sci. Philadelphia*, **16**: 203.

Fierasfer acus, Bleeker, 1879, *Verh. Akad. Amsterdam*, **18**: 21.

Fierasfer homii, Waite, 1897, *Mem. Austral. Mus.* **3**: 194.

Fierasfer microdon Gilbert, 1905, *Bull. U.S. Fish Comm.* **23** : 655. Jordan & Seale, 1905, *Bull. Bur. Fish.* **25** : 435.
Fierasfer homei, Steindachner, 1906, *SitzBer. Akad. Wiss. Wien*, **115** : 1419.
Fierasfer Sluiteri Weber, 1913, *Siboga-Expeditie*, **32** : 95.
? *Pirellinus lumbricoides*, Whitley, 1928, *Rec. Austral. Mus.* **16** : 226.
Carapus homei, Fowler & Bean, 1927, *Proc. U.S. nat. Mus.* **71** (10) : 15. Fowler, 1928, *Mem. Bishop Mus.* **10** : 445. Mukerji, 1932, *Rec. Indian Mus.* **34** : 567. Herre, 1936, *Publ. Field Mus. zool. Ser.* **21** : 416. Herre, 1939, *Rec. Indian Mus.* **41** : 574. Abe, 1939, *Palao trop. biol. Stud.* **1** : 574. de Beaufort & Chapman, 1951, *Fishes of the Indo-Australian Archipelago*, **9** : 4496. Smith, J. L. B., 1955, *Ann. Mag. nat. Hist.* (12) **8** : 414.
? *Fierasfer arenicola*, Borodin, 1930, *Bull. Vanderbilt oceanogr.* (*Mar.*) *Mus.* **1** : 62.
Fierasfer Mourlani Petit, 1934, *Bull. Mus. Hist. nat. Paris*, **6** : 393.
Carapus neglectus, Smith (J. L. B.), 1949, *Sea Fishes of Southern Africa* : 359. Smith (J. L. B.), 1955, *Ann. Mag. nat. Hist.* (12) **8** : 413.

The specimens examined include the type and 48 others (27 adults, 2 tenuis, the rest probably juveniles) in the collection of the British Museum. The localities represented are the Seychelles, Laccadives, Chagos Archipelago, Zanzibar, Dar-es-Salaam, Saya de Malha bank, Madras, Raiatea, Fiji, Tahiti, Rotuma, Samoa, Misol, New Guinea, Solomon Islands, Amboyna and Woosung.

Richardson studied three specimens, two obtained by Sir James Ross during the voyage of H.M.S. " Erebus " and " Terror " (one of which was dissected) and another sent to the Royal College of Surgeons from Timor, where it had been found in a holothurian. The locality of the first two specimens is unknown, though Richardson believed it might be Tasmania. However, this species has not subsequently been reported further south than the latitude of New Caledonia. Only one of the three specimens is still in existence and this is in the collection of the British Museum (Natural History), no. 1952.10.30.3. The type locality is generally stated as Tasmania but should probably be given as Timor.

Specific characters. Maximum length *c.* 200 mm. ; length of head one-sixth to about one-seventh of total length ; maximum depth of head one-half to three-fifths and maximum width two-fifths to one-half of length of head ; specimens less than 100 mm. long have relatively shorter and more slender heads than have larger specimens horizontal diameter of eye greater than length of snout, equal to interorbital width ; maxilla extends behind orbit to a distance equal to half horizontal diameter of eye ; one or two anterior teeth in upper jaw enlarged, the rest extremely small ; teeth of outermost series in lower jaw larger and stouter than those of inner series, bulging out a little beyond the edge of the jaw bone ; central row of usually three or four large, conical or slightly curved teeth on vomer, flanked by smaller ones ; pectoral fins half length of head ; anus anterior to roots of pectorals ; translucent in life with bluish or reddish shades anteriorly, dark cross-bars when adult (Jordan & Seale, 1905) ; silver spot between hind part of eye and maxilla in most specimens and a series of silver patches on flanks above lateral line. *Oxybeles lumbricoides* Bleeker is probably a tenuis larva of this species.

Measurements and proportions of the type and of representative adults are given in Table VI, and a summary of the principal measurements of the adults studied in Table VII.

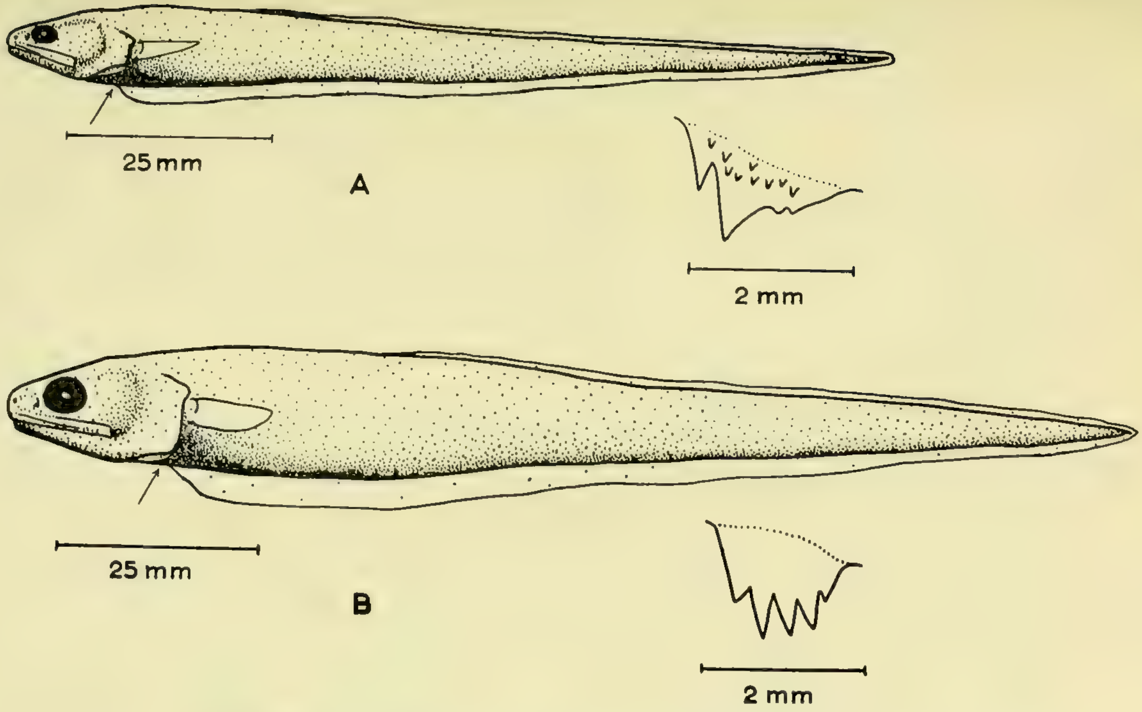


FIG. 11.—*Carapus homei* (Richardson). A, The type and its vomerine teeth ; B, a representative specimen from the Indian Ocean, and its vomerine teeth.

TABLE VI.—Carapus homei (*Richardson*). *Measurements and Proportions of the Type and of Representative Adults.*

Collection	British Museum					
Number	1952.10.30.3		1875.3.3.8		1908.3.23.36	
Locality	?		Samoa		Saya de Malha	
	mm.		mm.		mm.	
Total length	109*		142		139	
Length of head	16	(15% TL)	20	(14% TL)	22	(16% TL)
Maximum depth of head	9	(56% HL)	10	(50% HL)	12	(55% HL)
Maximum width of head	7	(44% HL)	7	(35% HL)	10	(45% HL)
Length of snout	3	(19% HL)	4	(20% HL)	4	(18% HL)
Horizontal diameter of eye	3·5	(22% HL)	5	(25% HL)	5	(23% HL)
Vertical diameter of eye	3	(19% HL)	4·5	(22% HL)	4·5	(20% HL)
Interorbital width	2·5	(16% HL)	4	(20% HL)	4	(18% HL)
Length of maxilla	8·5	(53% HL)	11	(55% HL)	11·5	(52% HL)
Length of pectoral fin	8	(50% HL)	13	(65% HL)	10	(45% HL)
Maximum depth of body	9	(56% HL)	13	(65% HL)	15	(68% HL)
Preanal length	14	(13% TL)	17	(12% TL)	20	(14% TL)

* Type specimen.

TL = total length ; HL = length of head.

TABLE VII.—Carapus homei (*Richardson*). *Summary of Measurements and Proportions of Adult Fish.*

Variate.	N.	R. mm.	$M \pm \sigma_M$. mm.
Total length	27	100–190	138·6±5·09
Length of head	27	15–30	20·0±0·76
Depth of head	27	8–16	10·2±0·61
Width of head	27	5–14	8·1±0·60
Length of pectoral fin	26	7–15	10·4±0·78
Preanal length	26	13–27	17·7±0·80
		%	%
Length of head (% TL)	27	12·8–17·0	14·6±0·19
Depth of head (% HL)	27	50·0–60·0	54·3±0·18
Width of head (% HL)	27	32·0–50·0	41·5±0·93
Length of pectoral (% HL)	26	40·0–65·0	50·6±0·89
Preanal length (% TL)	26	10·5–11·4	12·6±0·21

N = number of specimens ; R = range of variate ; M = mean of variate (± standard error of mean σ_M) ; TL = total length ; HL = length of head.

C. homei has a wide distribution and more extensive collections might show that it should be broken up into subspecies ; this, however, is not possible with the material at present available. It has been reported from Ghardaqa in the Red Sea, various Indian Ocean localities, Indonesian waters, the Philippines, Celebes, Torres Straits, off the coast of Queensland, Hawaii, Woosung, Palao and many localities in the South Pacific. It has been found mainly in species of *Holothuria*, *Actinopyga* and

Stichopus, but also occasionally in other echinoderms (*Culcita*, *Nardoa*) and lamellibranchs (*Cardium*, *Pinctada*) and once in an ascidian (*Styela*).

Several nominal species have been described from within the range of *C. homei*, which have differed from it solely in point of size and of number of vomerine teeth, neither of which, alone or together, can be regarded as good diagnostic characters. Two of these forms, *Fierasfer brandesii* Bleeker and *Fierasfer sluiteri* Weber, are now generally accepted as synonymous with *C. homei*, while two others, *Fierasfer microdon* Gilbert from Hawaii and *Fierasfer mourlani* Petit from Madagascar, are not distinguishable in description from the smaller specimens of *C. homei*. None of these four forms has been recorded by other than the original authors, but two others, *Fierasfer neglectus* Peters from Mozambique and *Fierasfer affinis* Günther of unknown origin, have been recorded upon a number of subsequent occasions and therefore merit more detailed consideration.

F. neglectus was well described, though not figured, and there are in the British Museum collection a number of fierasfers from Indian Ocean localities that are clearly referable to this species. However, this group bears an equally close resemblance to the *C. homei* specimens from Indo-Australian and Pacific waters, especially in the dentition and the general presence of a suborbital silver patch. Specimens of similar size from the two areas have almost identical proportions. The two groups show small differences but comparison shows these differences to be too small for it to be impossible for them to have been drawn from the same " population ". *F. neglectus* may ultimately be found to be subspecifically distinct, but with the material at present available it is not possible clearly to diagnose to which group, Indic or Pacific, any given specimen belongs.

F. affinis, of which the type only is known, has been regarded by most American authors as a fierasfer from American waters. This, however, is erroneous. It is 174 mm. in length, far larger than any fierasfer yet recorded from the coastal waters of Central America ; the dentition is wholly that of *C. homei* ; there is a suborbital silver spot ; and its dimensions fit closely with those of the available sample of *C. homei*, especially those of the Pacific group. Comparison of the main characters of this specimen with those of the available sample of *C. homei* give values of d/σ which are well below 3·0, the minimum value usually taken as suggesting specific difference (Simpson & Roe, 1947).

Carapus pindae Smith, 1955

Carapus pindae Smith (J. L. B.), 1955, *Ann. Mag. nat. Hist.* (12) 8 : 412.

The type, the only specimen known, was found inside an unidentified holothurian taken at Pinda (14° 10′ S., 40° 40′ E.) and is lodged in the Department of Ichthyology, Rhodes University, Grahamstown, South Africa. It has not been available for study and the following account is derived entirely from the original description.

SPECIFIC CHARACTERS. Total length 75 mm.; length of head one-seventh of total length ; width of head about one-third, depth of head about one-half, of length of head ; horizontal diameter of eye twice as great as interorbital width, one-half as great again as length of snout ; maxilla extending behind orbit for distance less than one-half horizontal diameter of eye ; teeth in single series in upper jaw, the first pair enlarged ; teeth in bands in lower jaw, none enlarged ; palatine teeth uniserial posteriorly, polyserial anteriorly ; two large and several small teeth on vomer ; pectoral fins slightly less than one-half length of head ; anus anterior to roots of pectoral fins ; translucent in life with pink sheen, abdomen silvery-bronze, row of silvery-bronze spots on sides of abdomen, faint dusky cross-bars on back.

The measurements of this specimen are not stated, but a series of proportions are given in the original description.

This species is closest to *C. homei*, but differs from it and all other fierasfers so far described in the partially uniserial nature of the dentition. Its small size suggests that *C. pindae* may not be fully mature, in which case the peculiarities of the dentition might be only transient. Should this indeed be the case, there seems little to justify separation of this species from *C. homei* as at present comprehended.

Carapus kagoshimanus (Steindachner & Döderlein), 1877

Fierasfer kagoshimanus Steindachner & Döderlein, 1877, *Denkschr. Akad Wiss. Wien.* **53** : 1. Jordan & Snyder, 1901, *Annot. zool. jap.* **3** : 118.

Carapus kagoshimanus, Jordan & Fowler, 1903, *Proc. U.S. nat. Mus.* **25** : 743. Franz, 1910, *Abhandl. Bayer Akad. Wiss., Suppl.* **4** : 31.

The type was obtained in the harbour at Kagoshima, Japan and its present whereabouts are unknown. No specimens have been available for study and the following account is based upon those of the authorities cited above.

Specific characters. Length of type 110 mm.: head one-seventh of total length ; maximum depth of head three-fifths, maximum width two-fifths, of length of head ; horizontal diameter of eye equal to length of snout and to interorbital width ; teeth of jaws, palatines and vomer small ; anus beneath base of pectoral fins ; pectorals less than half length of head ; colour stated as uniform pink with dark spots.

This species has been reported only from Kagoshima and Sagami.

Carapus owasianus Matsubara, 1953

Carapus owasianus Matsubara, 1953, *Jap. J. Ichthyol.* **3** : 29.

The type, the only specimen known, was taken free-swimming off the coast near Owasi, Japan, and placed in Matsubara's Fish Collection, no. 18871. It has not been available for study and the following account is compiled from the original description.

Specific characters. Total length about 200 mm. (determined from figure, not stated by author) ; head over one-eighth of total length ; horizontal diameter of eye a little greater than length of snout, nearly twice as great as interorbital width ; maxilla extending behind orbit for a distance approximately equal to half horizontal diameter of eye ; enlarged teeth at front of both jaws ; vomerine teeth small ; anus slightly posterior to roots of pectorals ; pectoral fins half length of head ; colour in life unknown.

The measurements of this specimen have not been recorded, but its detailed proportions are listed in the original publication.

Carapus houlti (Ogilby), 1922

Fierasfer houlti Ogilby, 1922, *Mem. Queensland Mus.* **7** : 301.
Carapus houlti, McCulloch, 1929, *Mem. Austral. Mus.* **5** : 354.

The two cotypes, the only specimens known, were taken together off Double Island Point, southern Queensland, in 36 fathoms (70 metres) enclosed in the remains of an unidentified holothurian. They have not been available for study and the following account is compiled from the original description.

SPECIFIC CHARACTERS. The two specimens were 283 mm. and 236 mm. long ; head one-seventh to one-eighth of total length ; width of head one-half its length ; maximum depth of body considerably greater than maximum depth of head ; teeth in jaws small and conical, uniform in size ; row of four large teeth on vomer ; anus beneath roots of pectorals ; pectoral fins a little less than one-third length of head ; colour greyish-brown with darker dots.

Carapus boraborensis (Kaup), 1856

Fierasfer boraborensis Kaup, 1856, *Arch. Naturges.* **22** : 97. Kaup, 1856, *Catalogue of Apodal Fishes* : 160.
Jordanicus boraborensis, Jordan & Seale, 1905, *Bull. Bur. Fish.* **25** : 435. Fowler, 1928, *Mem. Bishop Mus.* **10** : 446. Fowler, 1938, *Mon. Acad. nat. Sci., Philadelphia* **2** : 260.

The original description is based upon several specimens obtained by Lesson and Carnot at Borabora in the Samoan Archipelago and placed in the Paris Museum. They seem to be no longer in existence and no examples have been available for study.

SPECIFIC CHARACTERS. Kaup's two accounts are brief, unillustrated and in part contradictory. In the first the length is given as 330 mm., with the head one-eleventh of the total length and the pectoral fins one-third to one-quarter the length of the head; no other characters are mentioned. The second account records also the vomerine teeth and preanal length. In this description the largest specimen is said to be 23 in., or about 580 mm., in length ; the head is once again given as one-tenth to one-eleventh of the total length, but the pectoral fins are said to be one-sixth the length of the head. This fish has a cluster of thick teeth on the vomer and the anus is situated nearly 30 mm. anterior to the roots of the pectoral fins.

This may not be a single species, nor even a fierasfer at all. It has been included in lists of the Samoan fish fauna (Jordan & Seale, 1905 ; Fowler, 1928 & 1938), but the citations are from Kaup and the species has not been seen since. There is no evidence to justify the inclusion of this rather doubtful form in *Jordanicus*.

Carapus parvipinnis (Kaup), 1856

(Text-fig. 12)

Fierasfer parvipinnis Kaup, 1856, *Arch. Naturges.* **22** : 97. Kaup, 1856, *Catalogue of Apodal Fishes* : 160. Günther, 1862, *Catalogue of Fishes*, **4** : 381. Fowler, 1900, *Proc. Acad. nat. Sci., Philadelphia*, **1900** : 523. Kendall & Goldsborough, 1911, *Mem. Mus. comp. Zool. Harvard*, **26** : 330. Weber, 1913, *Siboga Expeditie*, **32** : 96. Tortonese, 1939, *Boll. Mus. Zool. Anat. comp. Torino*, **47** : 379.

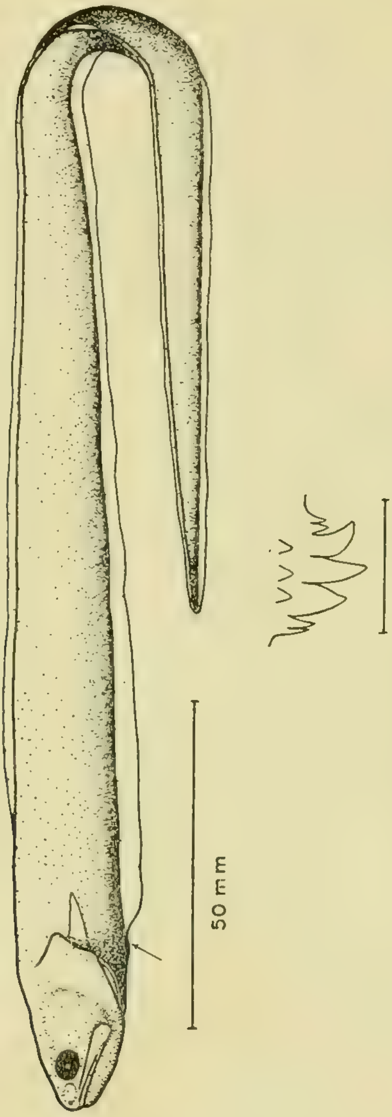


FIG. 12.—*Carapus parvipinnis* (Kaup). A representative specimen and its vomerine teeth.

Jordanicus parvipinnis, Jordan & Seale, 1905, *Bull. Bur. Fish.* **25** : 435. Fowler, 1925. *Proc. Acad. nat. Sci., Philadelphia*, **77** : 264. Fowler, 1928, *Mem. Bishop Mus.* **10** : 447. Fowler, 1938, *Mon. Acad. nat. Sci., Philadelphia*, **2** : 260.

Carapus parvipinnis, Herre, 1936, *Publ. Field Mus. zool. Ser.* **21** : 416. Abe, 1939, *Palao trop. biol. Stud.* **1** : 575. Herre & Herald, 1950, *Philipp. J. Sci.* **79** : 337. Smith (J. L. B.), 1955, *Ann. mag. nat. Hist.* (12) **8** : 412.

The study material includes 12 adults in the collection of the British Museum (Natural History) and one in that of the Universitetets Zoologiske Museum, Copenhagen. The localities represented are Tahiti, Ponapé, Samoa, Rotuma, Raiatea, Banda and Mauritius. The type was obtained by Quoy and Gaimard at Carteret Harbour and probably placed in the Paris Museum. It seems to be no longer in existence.

SPECIFIC CHARACTERS. Maximum length about 300 mm.; length of head one-ninth to less than one-tenth of total length ; maximum depth of head about two-fifths and maximum width about one-half of length of head ; eye well below dorsal profile of head ; its horizontal diameter half as long again as length of snout, slightly less than interorbital width ; maxilla very stout, extending behind orbit for a distance equal to horizontal diameter of eye ; jaw teeth small, nearly uniform, a few at front of lower jaw smaller than rest ; three or four large, stout, conical teeth on vomer, surrounded by smaller teeth ; pectoral fins one-third to one-quarter length of head ; anus anterior to roots of pectorals. Of four specimens obtained alive at Moorea Island, Tahiti, two were a warm red-brown colour, the other two pale and translucent (Herre, 1936*b*). One reddish fish was certainly adult ; the pale fish may have been juveniles.

Measurements and proportions of representative adults are given in Table VIII, and a summary for the adults examined in Table IX.

TABLE VIII.—Carapus parvipinnis (*Kaup*). *Measurements and Proportions of Representative Adults.*

Collection	British Museum.			
Number	1929.8.4.1.		1874.11.19.31.	
Locality	Tahiti.			
	mm.		mm.	
Total length	195		260	
Length of head	21	(11% TL)	28	(11% TL)
Maximum depth of head	13	(62% HL)	16	(57% HL)
Maximum width of head	13	(62% HL)	12	(43% HL)
Length of snout	3	(14% HL)	4·5	(16% HL)
Horizontal diameter of eye	4	(19% HL)	5	(18% HL)
Vertical diameter of eye	3·5	(17% HL)	4·5	(16% HL)
Interorbital width	5	(24% HL)	7·5	(27% HL)
Length of maxilla	10	(48% HL)	12·5	(45% HL)
Length of pectoral fin	6	(29% HL)	8	(29% HL)
Maximum depth of body	14·5	(69% HL)	16	(57% HL)
Preanal length	21	(11% TL)	27	(10% TL)

TL = total length ; HL = length of head.

TABLE IX.—Carapus parvipinnis (*Kaup*). *Summary of Measurements and Proportions of Adults.*

Variate.		R. mm.	M. mm.
Total length	10	167–295	224·9
Length of head	10	18–33	24·3
Depth of head	10	10–21	14·8
Width of head	10	8–21	12·6
Pectoral length	10	4–9	6·9
Preanal length	8	18–33	25·0
		%	%
Head length (% TL)	10	9·55–11·67	10·8
Head depth (% HL)	10	55·56–65·38	60·7
Head width (% HL)	10	42·10–63·64	51·8
Pectoral length (% HL)	10	19·05–37·50	28·3
Preanal length	8	9·05–11·19	10·6

N = number of specimens ; R = range of variate ; M = mean value of variate ; TL = total length ; HL = length of head.

This species has been assigned (Jordan & Seale, 1905) to *Jordanicus* on account of the relatively great width of the head, even though it possesses neither of the other characters—adnate maxillae and absence of a lower lip—by which this genus was originally separated from *Carapus*. Instead, *C. parvipinnis* closely resembles *C. acus* in the form of its vertebrae, the shape of the lower jaw and the nature of the dentition. The most striking difference between this species and the other *Carapus* spp. is the relatively small size of the head which, when combined with the cylindrical body form, does cause it to approach *Encheliophis* (*Jordanicus*) *gracilis* in general appearance. However, this resemblance is purely superficial and provides no grounds for placing *C. parvipinnis* in any genus but *Carapus*.

C. parvipinnis occurs in the tropical Pacific, especially at Tahiti, Samoa and the Philippine and Solomon Islands, as an inquiline of holothurians. One specimen in the collection of the British Museum was obtained in Mauritius. It has relatively longer pectorals than have the Pacific Ocean specimens, but this may be merely an individual peculiarity.

Carapus caninus (Günther), 1862

(Text-fig. 13)

Fierasfer caninus Günther, 1862, *Catalogue of Fishes*, **4** : 381. Sauvage, 1891, *Histoire Naturelle des Poissons* : 476.

Jordanicus caninus, Fowler, 1927, *Bull. Bishop Mus., Honolulu*, **38** : 30. Fowler, 1928, *Mem. Bishop Mus.* **10** : 447. Fowler, 1938, *Mon. Acad. nat. Sci. Philadelphia*, **2** : 260.

Jordanicus fowleri, Smith (J. L. B.) 1955, *Ann. Mag. nat. Hist.* (12) **8** : 402.

Carapus mayottae, Smith (J. L. B.) 1955, *Ann. Mag. nat. Hist.* (12) **8** : 415.

The following account is based upon a re-examination of the type, no. 1952.10.30.2 in the collection of the British Museum (Natural History) ; locality unknown.

Specific characters. Total length of type is 83 mm.; body slender and strongly compressed, but not deeper than head ; head one-seventh of total length ; maximum depth of head one-half and maximum width one-third of length of head ; horizontal diameter of eye equal to length of snout, half as great again as interorbital width ; maxilla extends behind orbit for a distance equal to half horizontal diameter of eye ; outer row of teeth of lower jaw tall, curved, well-separated from each other, those at the front the largest ; inner teeth of lower jaw small, conical, close-set ; teeth of upper jaw small, conical, pair at front greatly enlarged ; vomerine teeth in a single row as large as outermost teeth of lower jaw ; pectoral fins one-third length of head ; anus below roots of pectorals ; colour in life unknown.

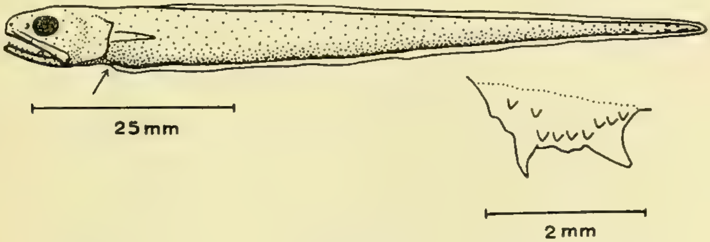


Fig. 13.—*Carapus caninus* (Günther). The type and its vomerine teeth.

Measurement of this specimen are given in Table X.

Table X.—Carapus caninus (*Günther*). *Measurements and Proportions of the type.*

Museum	British Museum.	
Number	1952.10.30.2.	
	mm.	
Total length	88	
Length of head	13	(15% TL)
Maximum depth of head	7	(54% HL)
Maximum width of head	4	(31% HL)
Length of snout	3	(23% HL)
Horizontal diameter of eye	3	(23% HL)
Vertical diameter of eye	2·5	(19% HL)
Interorbital width	2	(15% HL)
Length of maxilla	7·5	(57% HL)
Length of pectoral fin	5	(39% HL)
Maximum depth of body	6	(46% HL)
Preanal length	13	(15% TL)

TL = total length ; HL = length of head.

This species has also been recorded from Mayotte (Sauvage, 1891), host, if any, not stated ; and from Christmas Island (Fowler, 1927) when two specimens were taken in a pearl-oyster.

Smith (1955), believing that the type is no longer in existence, has suggested that the trivial name *caninus* should be abandoned and has proposed instead the names *Carapus mayottae* for the specimen from Mayotte and *Carapus fowleri* for those from Christmas Island. However, *Carapus caninus* is unquestionably valid and, though it has not been possible to examine the other specimens attributed to this species, the published descriptions and figures are not sufficiently at variance with Günther's type to warrant specific separation. Fowler's inclusion of *C. caninus* in *Jordanicus* is also incorrect.

Subgenus ***ONUXODON***

Subgeneric characters. Body strongly compressed, its greatest depth equal to length of head; interorbital strongly domed, its width less than horizontal diameter of eye; trunk vertebrae 19–20; swim-bladder partly calcified.

Key to Species

Pectoral fins less than one-quarter length of head . .	*C.* (*Onuxodon*) ***parvibrachium.***
Pectoral fins more than one-half length of head . .	*C.* (*Onuxodon*) ***margaritiferae.***

Carapus (Onuxodon) parvibrachium Fowler, 1927

(Text-fig. 14)

Carapus parvibrachium Fowler, 1927, *Bull. Bishop Mus.* **38** : 30. Fowler, 1928, *Mem. Bishop Mus.* **10** : 445.
Onuxodon parvibrachium, Smith (J. L. B.), 1955, *Ann. Mag. nat. Hist.* (12) **8** : 406.

The following account is based upon a single specimen obtained by Dr. T. Mortensen at Banda, Indonesia, and placed in the collection of the Universitetets Zoologiske Museum, Copenhagen. The holotype and one paratype were taken in Suva Bay, Fiji, in an unidentified clam-shell and placed in the Bernice P. Bishop Museum, Honolulu, Hawaii.

Specific characters. Total length 67 mm. (type and paratype were 81 mm. and 71 mm. respectively); length of head rather less than one-seventh of total length; maximum depth of head a little less than three-quarters and maximum width two-fifths of length of head; maximum depth of body equal to length of head; horizontal diameter of eye slightly greater than length of snout, two and a half times as great as interorbital width; maxilla extending behind orbit for a distance greater than horizontal diameter of eye; anterior pair of teeth in each jaw very large, the rest of the dentition minute; pectoral fins a little more than one-fifth length of head; translucent in life with pink sheen and dark markings on snout, at bases of dorsal and anal fins and on caudal region (Smith, 1955).

Measurements and proportions of this specimen are given in Table XI.

TABLE XI.—Carapus (Onuxodon) parvibrachium *Fowler. Measurements and Proportions of an Adult from Banda in the Collection of the Universitetets Zoologiske Museum, Copenhagen.*

	mm.	
Total length	67	
Length of head	9	(13% TL)
Maximum depth of head	7	(78% HL)
Maximum width of head	3·5	(39% HL)
Length of snout	2	(22% HL)
Horizontal diameter of eye	2·5	(28% HL)
Vertical diameter of eye	2	(22% HL)
Interorbital width	1	(11% HL)
Length of maxilla	6	(67% HL)
Length of pectoral fin	2	(22% HL)
Maximum depth of body	9	(100% HL)
Preanal length	11	(16% TL)

TL = total length; HL = length of head

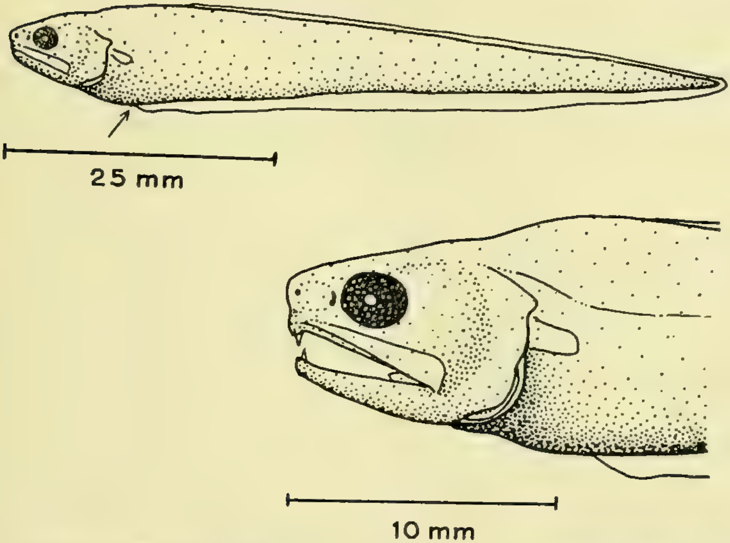


FIG. 14.—*Carapus* (*Onuxodon*) *parvibrachium* Fowler. A specimen from Bandu, Indonesia.

Carapus (Onuxodon) margaritiferae (Rendahl), 1921

(Text-fig. 15)

Fierasfer homei Weber, 1913, *Siboga Expeditie*, **32** : 95. (non Richardson, 1844, *Ichthyology of the Voyage of H.M.S. "Erebus" and "Terror"* : 73.)
Fierasfer margaritiferae Rendahl, 1921, *K. Svenska Vetensk. Akad. Handl.* **61** (9) : 5.
Carapus margaritiferae, de Beaufort & Chapman, 1951, *Fishes of the Indo-Australian Archipelago*, **9** : 449. Smith (J. L. B.), *Ann. Mag. nat. Hist.* (12) **8** : 400.
? *Fierasfer homei* (part), Abe, 1939, *Palao trop. biol. Stud.* **1** : 574.

The study material includes 11 adults in the collection of the Universitetets Zoologiske Museum, Copenhagen. Localities represented are Banda and Cape Jaubert. The type was taken from a pearl oyster dredged off Cape Jaubert, northwest Australia, and was placed in the Swedish Museum.

Specific characters. Greatest recorded length 92 mm.: length of head one-sixth to one-seventh of total length; maximum depth of head three-fifths and maximum width one-third of length of head; horizontal diameter of eye less than length of snout, twice as great as interorbital width; mouth nearly horizontal; maxilla extends behind orbit for a distance greater than horizontal diameter of eye; oval patch of many small teeth on vomer; pectoral fins one-half to three-fifths of length of head; translucent in life with pink sheen, caudal dusky (Smith, 1955).

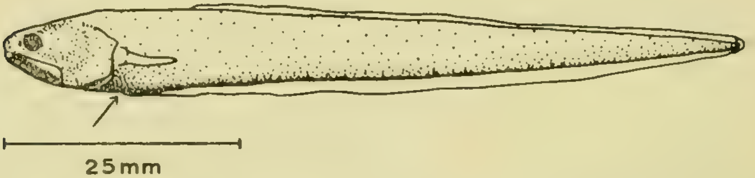


Fig. 15.—*Carapus* (*Onuxodon*) *margaritiferae* (Rendahl). A representative specimen from Cape Jaubert, Australia.

Measurements of representative specimens are given in Table XII, and a summary of measurements and proportions of the adult fish studied in Table XIII.

Table XII.—Carapus (Onuxodon) margaritiferae (*Rendahl*). *Measurements and Proportions of Representative Adults in the Collection of the Universitetets Zoologiske Museum, Copenhagen.*

Locality	Banda.		C. Jaubert.	
	mm.		mm.	
Total length	68		82	
Length of head	9	(13% TL)	12	(15% TL)
Maximum depth of head	5	(56% HL)	8	(67% HL)
Maximum width of head	3·5	(39% HL)	5	(42% HL)
Length of snout	2	(22% HL)	3	(25% HL)
Horizontal diameter of eye	1·3	(14% HL)	1·5	(21% HL)
Vertical diameter of eye	1	(11% HL)	2	(17% HL)
Interorbital width	0·7	(8% HL)	1·5	(12% HL)
Length of maxilla	5	(56% HL)	7	(58% HL)
Length of pectoral fin	6	(67% HL)	7	(58% HL)
Maximum depth of body	7	(78% HL)	9·5	(79% HL)
Preanal length	9·5	(14% TL)	12	(15% TL)

TL = total length; HL = length of head.

TABLE XIII.—Carapus (Onuxodon), margaritiferae (*Rendahl*).
Summary of Measurements and Proportions of Adults examined.

Variate.	N.	R. mm.	M. mm.
Total length	10	53–82	68·8
Length of head	10	5–12	9·3
Depth of head	10	3–8	5·7
Width of head	9	1·5–5	3·3
Length of pectoral fin	9	2–7	5·6
Preanal length	9	8–12	9·7
		%	%
Length of head (% TL)	10	8·93–15·38	13·23
Depth of head (% HL)	10	50·00–71·43	61·24
Width of head (% HL)	9	30·00–57·14	38·58
Pectoral length (% HL)	9	40·00–71·43	57·47
Preanal length (% TL)	9	13·11–14·47	13·59

N = number of specimen; R = range of variate; M = mean value of variate; TL = total length; HL = length of head.

C. margaritiferae has been found mainly in the Indo-Australian region, where it has been recorded from Cape Jaubert, Flores, Saleyer and Banda in the lamellibranchs *Avicula* and *Pteria*, in pearl oysters, and once in a holothurian. Five fierasfers taken at Palao (Abe, 1939) in *Pinctada maxima* may also belong to this species, while Smith (1955) has recorded it from clams at Durban.

Carapus reedi Smith, 1955

Carapus reedi Smith (J. L. B.), 1955, *Ann. Mag. nat. Hist.* (12) 8, p. 410.

The type, the only specimen known, was found in a clam shell taken in 2 fathoms at Durban and is lodged in the Department of Ichthyology, Rhodes University, Grahamstown, South Africa. It has not been available for study and the following account is based entirely upon the original description.

SPECIFIC CHARACTERS. Total length about 70 mm.; head about one-fourteenth of total length; maximum width of head about one-quarter, maximum depth nearly as great as length of head; diameter of eye equal to length of snout, twice as great as interorbital width; maxilla extends only as far as posterior edge of orbit; jaw and palatine teeth small, uniserial; anterior pair of teeth in each jaw enlarged; vomerine teeth few, small; pectoral fins two-thirds length of head; anus posterior to base of pectorals; translucent in life with pink sheen, few black spots on top of head.

Measurements of this specimen have not been published, but detailed proportions are given in the original description.

This specimen is clearly not a vexillifer larva, as are so many of the apparently aberrant fierasfers that have been described, but its small size, short maxilla, uniserial dentition and relatively short head form a combination of characters which suggest that it has not yet attained full maturity. From the illustration it is undoubtedly a *Carapus*, while the proportions of the head suggest that it should be placed in the subgenus *Onuxodon*. If it is indeed a late tenuis larva or early juvenile, it is probably attributable to the preceding species, *C. margaritiferae*.

Genus ***ECHIODON*** Thompson, 1837

Genotype ***Echiodon Drummondii*** Thompson, 1837

Echiodon Thompson, 1837, *Proc. zool. Soc. Lond.* **5** : 55. Type species *Echiodon Drummondii* Thompson, 1837.
Ophidium (*Echiodon*), Thompson, 1841, *Trans. zool. Soc. Lond.* **2** : 207.

GENERIC CHARACTERS. Body elongated, cylindrical; lateral processes of first and second vertebrae expanded, not fused; processes of all other vertebrae small and not expanded; trunk vertebrae number 27–28; lower jaw stout, nearly straight, narrowing at distal end, then expanding again at extreme tip; one or two pairs of large, fang-like teeth at front of both jaws; other jaw teeth small and close-set in narrow bands; anterior fangs of lower jaw separated from other teeth by a large diastema; maxilla extending beyond orbit in adult, clearly outlined by folds of skin; anus posterior to roots of pectorals in adult; upper edge of orbit impinging on dorsal profile of skull; swim-bladder long and straight, not constricted; branchiostegals 7.

The genus *Echiodon* was first created to contain the newly discovered species *E. drummondi*. Subsequently, its author reduced it to subgeneric rank under *Ophidium* and Kaup (1856*a*) united it with *Fierasfer*. Later authors have followed Kaup, but the differences between *E. drummondi* and most other fierasfers are so clear-cut that it is necessary to re-establish the genus, not only for the original species, but also for that originally described as *Ophidium dentatum* Cuvier (1817).

Echiodon differs from both *Carapus* and *Encheliophis* in both vertebral and jaw structure, in the clearly posterior position of the anus in the adult and in the presence of a diastema at the front of both jaws. It is further distinguished from *Encheliophis* in the possession of polyserial dentition and from *Carapus* in the relative shortness of the head.

KEY TO SPECIES, ADULTS ONLY

Upper profile of head rounded vomer tapering posteriorly; no gap between vomerine and palatine teeth . . . . *E. drummondi*
Upper profile of head straight; vomer rounded posteriorly; distinct gap between vomerine and palatine teeth . . . . *E. dentatus*

Echiodon drummondi Thompson, 1837

(Text-fig. 16)

Echiodon drummondii Thompson, 1837, *Proc. Zool. Soc. Lond.* **5** : 52. Yarrell, 1852, *Proc. Zool. Soc. Lond.* **20** : 14. Edward, 1863, *Zoologist* (1) **21** : 8495. Couch, 1864, *History of the Fishes of the British Isles*, **3** : 133.
Ophidium (*Echiodon*) *drummondii*, Thompson, 1841, *Trans. zool. Soc. Lond.* **2** : 207.

Fierasfer dentatus Kaup, 1856, *Catalogue of Apodal Fish* : 157. (non *Ophidium dentatum* Cuvier, 1817, *Règne Animal*, **2** : 239.) Günther, 1862, *Catalogue of Fishes*, **4** : 381. Day, 1880, *The Fishes of Great Britain and Ireland*, **1** : 228. Colett, 1882, *Forh. VidenskSelsk., Kristiania*, **1882**, (19) : 5. Sim. 1883, *Scottish Nat.*, **7** : 55. Fries, Ekström & Sundevall, 1893, *History of Scandinavian Fishes.* **2** : 260. Aflalo, 1904, *British Salt-water Fish* : 294. Ehrenbaum-Helgoland, 1909, *Nord Plank.* **10** : 217. Grieg, 1911, *Bergen Mus. Aarbok.* **1911** (6) : 17. Ehrenbaum-Helgoland, 1936, *Naturgeschichte und Wirtschaftliche Bedeutung der Seefische Nordeuropas* : 15.

The following account is based upon 132 adults in the collection of the Scottish Home Department's Laboratory at Torrey, Aberdeen, obtained mainly from the coastal waters of north and west Scotland and Northern Ireland, and three late vexillifers in the collection of the British Museum (Natural History), obtained at Banff. The type was found dead on a beach at Glenarm, Co. Antrim, Northern Ireland. It can no longer be traced.

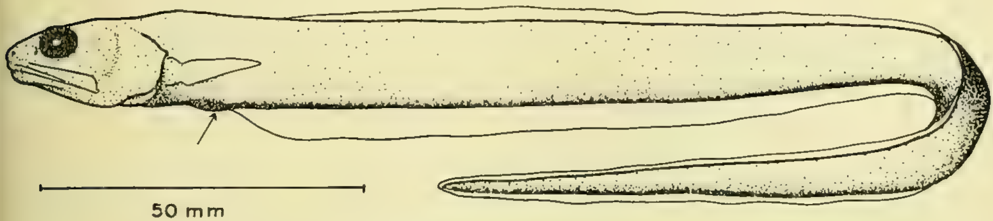


FIG. 16.—*Echiodon drummondi* Thompson. A representative specimen from Scottish waters.

SPECIFIC CHARACTERS. Greatest recorded length 300 mm.; length of head one-ninth to one-eleventh of total length ; maximum depth of head about one-half and maximum width about one-third of length of head ; upper profile of head convex ; horizontal diameter of eye slightly greater than length of snout, about twice as great as interorbital width ; maxilla extends well behind posterior edge of orbit ; anus 3–5 mm. posterior to roots of pectoral fins ; pectorals about three-fifths length of head ; patch of teeth on vomer rounded anteriorly, tapering posteriorly and merging with bands of palatine teeth ; colour in life believed to be reddish, with silvery abdomen, operculum and iris and dark markings on top of head, along edges of median fins and on tip of tail. (Silvery regions and dark markings are usually visible in preserved specimens.)

There is a vexillifer larva, resembling adult in form of lower jaw and in dentition. It is translucent in life, with reddish colour along dorsal and ventral surfaces, silvery spot near anus, dark-green pupil and silvery iris (Edward, private communication, cited by Couch, 1864). Eggs and other stages in the life history are unknown.

Measurements and proportions of representative adults are given in Table XIV, and a summary for the specimens examined in Table XV.

TABLE XIV.—Echiodon drummondi *Thompson. Measurements and Proportions of Representative Adults.*

Locality.	61° 01′ N., 00° 30′ W. in 155 m. mm.	 mm.	Adriatic. mm.
Total length	215	250	200
Length of head	24 (11% TL)	25 (10% TL)	22·5 (11% TL)
Maximum depth of head	10 (42% HL)	12 (48% HL)	10 (44% HL)
Maximum width of head	8 (33% HL)	9 (36% HL)	7 (31% HL)
Length of snout	4 (15% HL)	6 (24% HL)	4·5 (20% HL)
Horizontal diameter of eye	5 (21% HL)	6 (24% HL)	5 (22% HL)
Vertical diameter of eye	4 (17% HL)	4·5 (18% HL)	4 (18% HL)
Interorbital width	2·5 (10% HL)	4 (16% HL)	4 (18% HL)
Length of maxilla	10·5 (44% HL)	13 (52% HL)	11·5 (51% HL)
Length of pectoral fin	14 (58% HL)	15 (60% HL)	13 (58% HL)
Maximum depth of body	10 (42% HL)	12 (48% HL)	10 (44% HL)
Preanal length	26 (12% TL)	32 (13% TL)	24 (12% TL)

TL = total length ; HL = length of head.

TABLE XV.—Echiodon drummondi *Thompson. Summary of Measurements and Proportions of Adults.*

Variate.	N.	R. mm.	M ± σ_M. mm.
Total length	104	160–292	257·1±2·59
Length of head	114	15–30	25·4±0·26
Depth of head	114	8·15	12·1±0·14
Width of head	108	6·13	9·7±0·14
Pectoral length	114	10–20	15·0±0·19
Preanal length	112	20–38	30·7±0·34
		%	%
Length of head (% TL)	104	9·09–11·73	10·31±0·05
Depth of head (% HL)	114	40·00–56·00	47·48±0·28
Width of head (% HL)	108	23·26–46·43	38·14±0·36
Pectoral length (% HL)	114	41·27–46·43	58·89±0·56
Preanal length (% TL)	102	11·11–14·80	12·48±0·04

N = number of specimens ; R = range of variate ; M = mean of variate (± standard error of mean, σ_M) ; TL = total length ; HL = length of head.

Echiodon drummondi is apparently not uncommon in the coastal waters round the north and west coasts of the British Isles and has been taken at a considerable number of localities at depths down to 100 fathoms (200 metres). It has also been reported from Scandinavian waters. A specimen from the Oceanographic Institute at Split is also assigned to *E. drummondi*, though it may ultimately prove to be subspecifically distinct. The measurements of this specimen are given in Table XIV.

Cuvier described two fierasfers from the Mediterranean of which one, *Ophidium* *imberbe,* is that now termed *Carapus acus.* The other, *Ophidium dentatum* Cuvier, 1817, was said to differ from the first and more common species only by the presence of " deux dents en crochets ", a character which barely constitutes a recognizable description. Kaup (1856*a*) examined a number of specimens of *O. dentatum,* at that time preserved in the Paris Museum, and concluded that Cuvier's Mediterranean and Thompson's Atlantic fierasfer were identical. Both have therefore been recorded by later authors as *Fierasfer dentatus,* the name used by Kaup.

Though *C. acus* is fairly common in the Mediterranean, the other fierasfer is extremely rare and known from only a few localities. I have been able to examine only two, one from Monaco and another, very poorly preserved, from Sicily. The Atlantic fierasfer is also generally regarded as extremely rare and has even been mentioned by some authors as an exotic stray from the Mediterranean ; but during the past fifty years (excluding the war periods) the research vessels of the Aberdeen Laboratory have obtained well over 100 adult fish which accord well with the description given by Thompson.

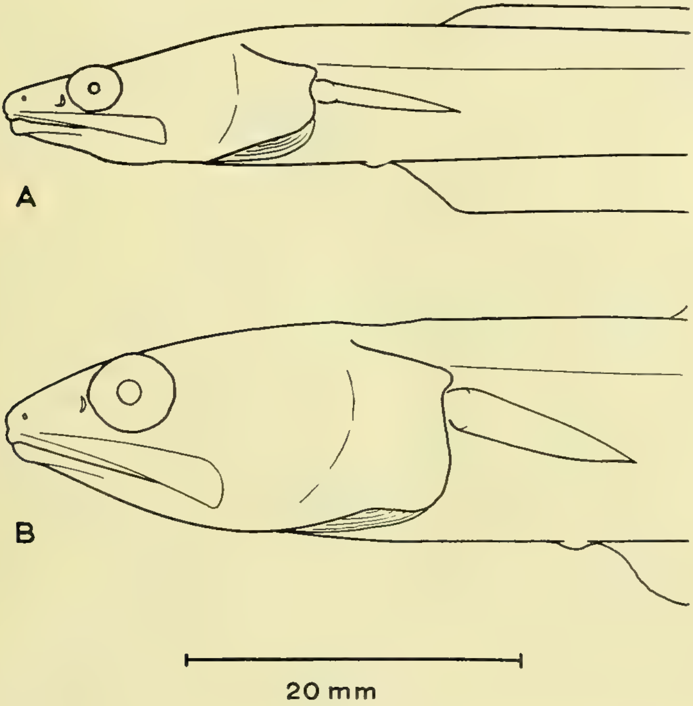


FIG. 17.—Heads of *Echiodon* spp. A, *E. dentatus* ; B, *E. drummondi.*

It is almost certain that Cuvier's types, assuming they were indeed the specimens seen by Kaup, are no longer in existence ; certainly they are not in the Paris collection. Thompson's specimen has also disappeared. It is therefore impossible to determine the status of these two forms by comparison of types, but from examination of the specimens preserved at Aberdeen and Monaco conforming to the description of *E. drummondi* and *O. dentatum* respectively it is clear that they are in fact two different species. They closely resemble each other in the structure of the lower jaw and of the first three vertebrae, in the presence of fang-like teeth at the front of both jaws and in the posterior position of the anus. However, they differ greatly in their dimensions and to a certain extent in their proportions. Other differences are apparent in the shape of the head, the obliquity of the mouth and the form of the operculum (Text-fig. 17). A further difference lies in the shape of the vomer, as displayed by the teeth it bears. In the Atlantic form the vomer tapers posteriorly, and there is no gap between vomerine and palatine teeth ; in the Mediterranean species the vomer terminates abruptly and its teeth are separated from those of the palatines by a well-marked gap.

Echiodon dentatus (Cuvier), 1817

(Text-fig. 18)

Ophidium dentatum Cuvier, 1817, *Règne Animal*, **2** : 239.

Fierasfer dentatus, Kaup, 1856, *Verh. phys.-med. Ges. Wurzburg*. **7** : 233. Kaup, 1856, *Arch. Naturges*, **22** : 93. Giglioli, 1880, *Esposizione di Pesca* : 97. Emery, 1880, *Fauna u. Flora Neapel*, **2** : 17. Carus, 1885, *Prodromus Faunae Mediterranea*, **2** : 580. Raffaele, 1888, *Mitt. zool. Stat. Neapel*, **8** : 1. Moreau, 1891, *Histoire Naturelle des Poissons de la France, Supplément* : 59. Belotti, 1891, *Atti Soc. ital. Sci. nat. Milano*, **33** : 127. Moreau, 1892, *Manuel d'Ichthyologie Française* : 405.

The following account is based upon one specimen in the collection of the Institut Océanographique, Monaco ; locality, Monaco : and another in the collection of the Universitetets Zoologiske Museum, Copenhagen ; locality Sicily.

Cuvier stated that his fish came from the Mediterranean. He did not designate a type and it is not certain that his specimens were preserved. The specimens examined by Kaup came, he believed, from Naples, but seem to be no longer in existence.

Specific characters. Total length 170 mm.; length of head one-ninth of total length ; upper profile of head straight ; maximum depth of head two-fifths, and maximum width one-third, of length of head ; horizontal diameter of eye slightly less than length of snout, nearly twice as great as interorbital width ; anus 4 mm. posterior to roots of pectorals ; pectoral fins slightly less than one-half length of head ; maxilla extends behind eye for distance equal to horizontal diameter of eye ; vomer rounded posteriorly ; vomerine and palatine teeth separated by a distinct gap ; colour in life unknown. Eggs attributable to this species have been described (Raffaele, 1888).

Measurements of this specimen are given in Table XVI. *Echiodon dentatus* has been recorded from Nice, Monaco, Naples, Sicily and the Adriatic.

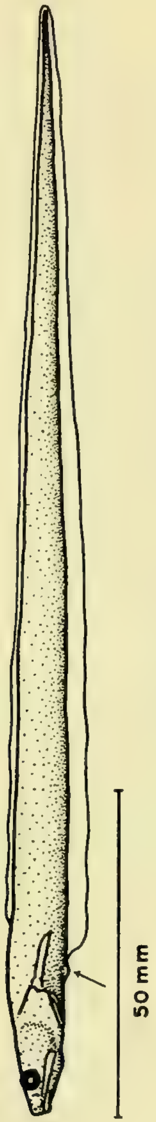


FIG. 18.—*Echiodon dentatus* (Cuvier). A specimen from Monaco.

TABLE XVI.—Echiodon dentatus (*Cuvier*). *Measurements and Proportions of a Specimen in the Collection of the Institut Océanographique de Monaco.*

	mm.	
Total length	170	
Length of head	19	(11% TL)
Maximum depth of head	8	(42% HL)
Maximum width of head	6	(32% HL)
Length of snout	3·5	(18% HL)
Horizontal diameter of eye	3·2	(17% HL)
Vertical diameter of eye	2·5	(14% HL)
Interorbital width	2	(11% HL)
Length of maxilla	10	(53% HL)
Length of pectoral fin	9	(47% HL)
Maximum depth of body	9	(47% HL)
Preanal length	23	(14% TL)

TL = total length ; HL = length of head.

SPECIES POSSIBLY ATTRIBUTABLE TO *ECHIODON*

Carapus rendahli Whitley, 1941

Fierasfer sp., Rendahl, 1925, *Vidensk. Medd. Dansk. Nat. Foren.* **81** : 13.
Carapus rendahli Whitley, 1941, *Austral. Zool.* **10** : 40.

The type, the only specimen known, was obtained at Port Jackson, New South Wales, and is now in the Australian Museum, no. I.2, 411. It has not been available for study and the following account is compiled from Whitley (1941).

SPECIFIC CHARACTERS. Total length 93 mm.; length of head less than one-eighth of total length ; maximum depth of head a little less than one-half and maximum width one-quarter of length of head ; horizontal diameter of eye as great again as length of snout, three times interorbital width ; maxilla extends a short distance behind orbit ; anus about 3 mm. posterior to roots of pectorals ; pectoral fins one-quarter length of head ; colour in life unknown. A number of vexillifers from New South Wales waters were provisionally attributed to this species.

The specimen is small and so may not be fully adult. The tip of the tail is broken off and a portion of the intestine protrudes through the anus. The general appearance as figured by Whitley is not that of a *Carapus*, but of a fish closely resembling *Echiodon drummondi*. The correspondence with *Echiodon* is shown also by the presence of fang-like teeth at the front of the jaws and by the posterior position of the anus, but cannot be proved without reference to the vertebral and jaw structure, neither of which have been described. It is not clear from the figure whether this specimen has a diastema in the lower jaw. Two further points suggesting that *C. rendahli* may in fact be an *Echiodon* are provided by the broken tail and intestinal prolapse. Damage to the tail is frequent in *Echiodon* and nearly 10% of the *E. drummondi* in the Aberdeen collection have broken or regenerating tails. On the other hand, *Carapus* spp. have seldom been found with broken tails, never with the tail stump showing signs of regeneration. Prolapse is also frequent in preserved *Echiodon drummondi*, unknown in *Carapus* spp. These two characters are not, of course, diagnostic, but are extremely suggestive.

Carapus cinereus Smith, 1955

Carapus cinereus Smith (J. L. B.), 1955, *Ann. Mag. nat. Hist.* (12) **8** : 409.

The type, the only specimen known, was taken in a tide pool at Inhaca Island (26° S., 33° D.) and is preserved in the Department of Ichthyology, Rhodes University, Grahamstown, South Africa. It has not been available for study and the following account is derived entirely from the original publication.

Specific characters. Total length 215 mm.; length of head less than one-ninth of total length ; maximum width of head two-fifths, maximum depth about one-half of length of head ; diameter of eye less than length of snout, greater than interorbital width ; maxilla extends behind eye for distance equal to about one-half diameter of orbit ; teeth of jaws small, blunt, conical, arranged in bands which terminate well before symphysis ; large, curved teeth at front of both upper and lower jaws, from description apparently separated by a diastema from other teeth ; vomerine teeth conical, of several sizes ; palatine teeth conical, generally small ; pectoral fins about one-half length of head ; anus clearly posterior to base of pectorals ; translucent in life with pink sheen, abdomen silvery, top of head dusky.

Apart from the total length the measurements of this specimen have not been published, but proportions are listed in the original paper.

The extreme length, relatively short head and cylindrical body of this specimen are characters which, though shown to a certain extent by *C. parvipinnis*, are by no means typical of the genus *Carapus*. The nature of the lower jaw and dentition are sufficient to exclude this species from *Encheliophis*, and its general appearance and the presumed presence of a diastema between the large anterior teeth and small posterior teeth in both jaws suggest that in fact this species should be assigned to *Echiodon*. The posterior position of the anus, the shape of the head, flatness of the interorbital and impingement of the upper edge of the orbit upon the dorsal profile of the head are further characters in which this form differs from veritable *Carapus* spp. and resembles *E. drummondi*.

Genus ***ENCHELIOPHIS*** Müller, 1842

Type species ***Encheliophis vermicularis*** Müller, 1842

Encheliophis Müller, 1842, *Ber. Verh. Preuss. Akad.* **1842** : 205. Type species *Encheliophis vermicularis* Müller, 1842.

Jordanicus Gilbert, 1905, *Bull. U.S. Fish. Comm.* **23** : 655. Type species *Fierasfer umbratilis* Jordan & Evermann, 1902, *Bull. U.S. Fish. Comm.* **22** : 206.

Encheliophiops Reid, 1940, *Rep. Allan Hancock Pacific Exp.* **9** : 47. Type species *Encheliophiops hancocki* Reid, 1940.

Generic characters. Body elongated, cylindrical ; lateral processes of first and second vertebrae long, not expanded ; of third, fourth and fifth vertebrae long, expanded and fused into broad plates ; of sixth and subsequent vertebrae short, not expanded ; trunk vertebrae 30–31 ; lower jaw slender, curved, tapering to tip ; teeth in single rows on jaws and palatines even in adult ; no diastema ; no fleshy lip to lower jaw ; maxilla concealed beneath skin ; interorbital domed, raising upper profile of skull considerably above orbit ; pectorals small or absent, but pectoral girdle always present ; anus beneath roots of pectoral in adult ; branchiostegals 6 or 7.

This genus was created to contain a finless fierasfer, *Encheliophis vermicularis*, from the Philippines. Subsequently other finless forms have been described from localities off the Pacific coast of Central America. One of these species, *E. hancocki*, introduced a new generic name *Encheliophiops*. This genus was separated from *Encheliophis* solely on the grounds that the only specimen known had the tip of the tail finless. This character, however, is shown by certain of the tenuis larvae of *Carapus acus* and by itself cannot be regarded as adequate for generic separation. *Encheliophiops* is accordingly regarded as synonymous with *Encheliophis*.

Also included with *Encheliophis* in the present work are the species customarily assigned to the genus *Jordanicus*. This genus was created to contain the single species *Fierasfer umbratilis* (generally accepted as a synonym for *Oxybeles gracilis*) and was stated to differ from other genera in the uniserial dentition, concealed maxilla and absence of a lip in the upper jaw. Radiographs of the type and other specimens of *Oxybeles gracilis* have added the structure of the lower jaw and fusion between the 3rd, 4th and 5th vertebrae to the original characters. In all these features the species assigned to *Jordanicus* differ from all other fierasfers except species of *Encheliophis*. The only difference which it has been possible to detect between *Encheliophis* and *Jordanicus* is the absence in the former of pectoral fins. However, the pectoral fins of *Jordanicus* are relatively far smaller than those of *Carapus* spp. and obvious though the presence of pectoral fins is as a diagnostic character, it is considered that this difference, unsupported by other characters, is insufficient to warrant generic distinction. The two genera are accordingly united, *Encheliophis* Müller, 1842, taking precedence over *Jordanicus* Gilbert, 1905. *Jordanicus* is retained, however, as a subgenus under *Encheliophis*.

Subgenus ***ENCHELIOPHIS***

SUBGENERIC CHARACTERS. Pectoral fins absent ; branchiostegals 6.

KEY TO SPECIES

1.	Membranes of dorsal and anal fins continuous round tip of tail	2
	Membranes of dorsal and anal fins not continuous round tip of tail	*E. hancocki*
2.	Body darkly pigmented	*E. vermicularis*
	Body not darkly pigmented	*E. jordani*

Encheliophis vermicularis Müller, 1842

(Text-fig. 19)

Encheliophis vermicularis Müller, 1842, *Ber. Verh. preuss. Akad. Wiss.* **1842** : 205. Müller, 1843 *Abhandl. Akad. Wiss. Berlin*, **1843** : 109. Kaup, 1856, *Catalogue of Apodal Fish* : 157. Günther, 1862, *Catalogue of Fishes*, **4** : 381. Herre, 1936, *Publ. Field Mus. zool. Ser.* **21** : 417. Abe, 1939, *Palao trop. biol. Stud.* **1** : 574. Smith (J. L. B.), 1955, *Ann. Mag. nat. Hist.* (2) **8** : 416.

Enchelyophis vermicularis Müller, 1843, *Arch. Naturges.* **9** : 329.

The study material includes a single specimen in the collection of the Universitetets Zoologiske Museum, Copenhagen, from Sambelong, mouth of the Ganges; and two in the British Museum (Natural History) obtained off Lizard Island, Great Barrier Reef, and at Tahiti. The type was obtained in the Philippines. It is uncertain whether it is still in existence.

Specific characters. The following description is of the specimen obtained at Sambelong by the *Galathea* expedition and placed in the Universitetets Zoologiske Museum.

Total length 79 mm. (greatest recorded for this species 175 mm.); head one-eleventh of total length; maximum depth of head two-fifths and maximum width rather less than one-third of length of head; horizontal diameter of eye slightly less than length of snout, slightly more than interorbital width; maxilla extends behind orbit for a distance equal to half horizontal diameter of eye; preanal length equals length of head; dark brown in life (Müller, 1842). Life history unknown.

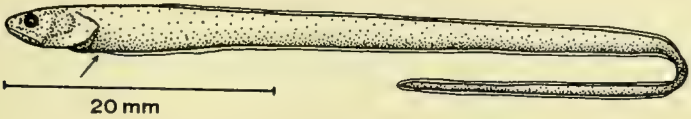


Fig. 19.—*Encheliophis vermicularis* Müller. A specimen from Sambelong, India.

Measurements of this and another specimen are given in Table XVII.

Table XVII.—Encheliophis vermicularis *Müller. Measurements and Proportions.*

Collection	Danish Museum.	British Museum.
Number	—	1933.8.12.47.
Locality	Sambelong.	Lizard Is.
	mm.	mm.
Total length	79	134
Length of head	7 (9% TL)	11·5 (9% TL)
Maximum depth of head	3 (43% HL)	5·5 (48% HL)
Maximum width of head	2 (29% HL)	4 (35% HL)
Length of snout	1·3 (19% HL)	2 (17% HL)
Horizontal diameter of eye	1·1 (16% HL)	2 (17% HL)
Vertical diameter of eye	1 (14% HL)	1·7 (17% HL)
Length of maxilla	3 (43% HL)	6 (52% HL)
Interorbital width	1 (14% HL)	2 (17% HL)
Maximum depth of body	3·5 (50% HL)	6 (72% HL)
Preanal length	7 (9% TL)	12 (9% TL)

TL = total length; HL = length of head.

E. vermicularis has been recorded from the coasts of Somaliland and India, the Philippines, Palao, Sulu Sea and Tahiti. It was taken in holothurians in the Philippines and is said to feed upon the viscera of its host (Semper, 1861).

Encheliophis jordani Heller & Snodgrass, 1903

Encheliophis jordani Heller & Snodgrass, 1903, *Proc. Acad. Sci. Washington*, **5** : 220.

The type, the only specimen known, was obtained at Tagus Cove, Albermarle Island, during the Hopkins Stanford Galapagos Expedition and deposited in Leland Stanford Junior University Museum, catalogue no. 6345. It has not been available for study and the following account is based upon the original description.

SPECIFIC CHARACTERS. Total length 114 mm.; length of head one-eleventh of total length ; maximum depth of head one-half its length, maximum width not stated ; horizontal diameter of eye less than snout length, slightly more than interorbital width ; maxilla extending short distance behind orbit ; small, rounded, patch of teeth on vomer ; anus below posterior border of operculum ; head and body dusky pink in life, abdomen silver, tail greyish-lavender, iris greenish-grey ; colours fading on preservation. Life history unknown.

Encheliophis hancocki (Reid), 1940

Encheliophiops hancocki Reid, 1940, Rep. *Allan Hancock Pacific Exp.* **9** : 47. Steinbeck & Ricketts, 1941, *Sea of Cortez :* 575.

The type was taken among the coral *Pocillipora* sp. at Gorgona Island, Columbia, during the course of the Hancock Pacific Expedition, 1935, and placed in the United States National Museum, catalogue no. 101789. It has not been available for study.

SPECIFIC CHARACTERS. Total length of type 74·8 mm.; length of head one-eleventh of total length ; maximum depth one-half and maximum width two-fifth of length of head ; horizontal diameter of eye equal to length of snout, slightly greater than interorbital width ; maxilla extends slightly behind orbit ; vomerine teeth not described ; anus about 2 mm. behind hind border of operculum ; median fins not continuous round tip of tail, which ends in a bare point : colour in life unknown. Life history unknown.

A second specimen was obtained from the cloaca of *Holothuria lubrica* taken in the Gulf of California (Steinbeck & Ricketts, 1941).

The status of the species of *Encheliophis* is doubtful and it is not entirely clear to which the various recorded specimens ought to be assigned. Certainly there is one fierasfer, *Encheliophis vermicularis*, which lacks paired fins, but though the majority of specimens noted by other authors have been ascribed to this species, they have not been figured, nor have their measurements been recorded. In consequence it has not been possible to build up a body of data giving some picture of the species as a whole, as has been the case with other members of the Carapidae.

The species of *Encheliophis* do not, so far as is at present known, differ greatly in proportions or in dentition and separation is based mainly upon colour. This is not a good criterion, but is the best available. Certainly, the dark pigmentation of *E. vermicularis*, which persists on preservation, makes it easy to distinguish this species from the paler *E. jordani*. *E. jordani* and *E. hancocki* resemble each other very closely indeed, and may ultimately prove to be conspecific.

Subgenus ***JORDANICUS***

SUBGENERIC CHARACTERS. Pectoral fins present, small; branchiostegals 7.

KEY TO SPECIES (ADULTS ONLY)

Vomerine teeth in single short median row	*E.* (*Jordanicus*) *gracilis*
Vomerine teeth in short band of about four rows . . .	*E.* (*Jordanicus*) *sagamianus*

Encheliophis (Jordanicus) gracilis (Bleeker), 1856

(Text-fig. 20)

Oxybeles gracilis Bleeker, 1856, *Nat. Tijdschr. Ned.-Ind.* **11** : 105. Doleschall, 1858, *Nat. Tijdschr. Ned.-Ind.* **15** : 163.

Fierasfer gracilis, Günther, 1862, *Catalogue of Fishes*, **4** : 381. Pietschmann, 1938, *Bull. Bishop Mus.* **156** : 51. Tortonese, 1939, *Boll. Mus. zool. Anat. comp. Torino*, **47** : 379.

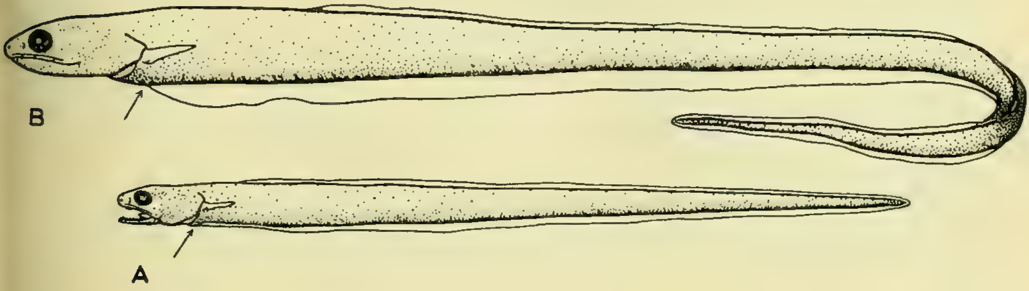
Fierasfer punctatus Fischer, 1885, *Jahrb. Hamburg Wiss. Anst.* **2** : 74. Barnard, 1927, *Ann. S. Afr. Mus.* **21** : 884.

Fierasfer umbratilis Jordan & Evermann, 1902, *Bull. U.S. Fish. Comm.* **22** : 206. Jordan & Evermann, 1903, *Bull. U.S. Fish. Comm.* **23** : 505.

Jordanicus umbratilis Gilbert, 1905, *Bull. U.S. Fish. Comm.* **23** : 655.

Fierasfer frantii Popta, 1912, *Notes Leyden Mus.* **23** : 185.

Carapus gracilis, Fowler, 1925, *Proc. Acad. nat. Sci. Philadelphia*, **77** : 283. Fowler, 1926, *Ann. Natal Mus.* **5** : 402. de Beaufort & Chapman, 1951, *Fishes of the Indo-Australian Archipelago*, **9** : 449.



25 mm

FIG. 20.—*Encheliophis* (*Jordanicus*) *gracilis* (Bleeker). A, The type; B, a more fully adult specimen.

Fierasfer (*Jordanicus*) *gracilis*, Barnard, 1927, *Ann. S. Afr. Mus.* **21** : 884.

Jordanicus gracilis, Fowler, 1928, *Mem. Bishop Mus.* **10** : 447. Fowler, 1931, *Mem. Bishop Mus.* **11** : 364. Fowler, 1934, *Mem. Bishop Mus.* **11** : 447. Abe, 1939, *Palao trop. biol. Stud.* **1** : 575. Schultz, 1943, *Bull. U.S. nat. Mus.* **180** : 287. Smith (J. L. B.), 1949, *Sea Fishes of Southern Africa* : 359. Smith (J. L. B.), 1955, *Ann. Mag. nat. Hist.* (12) **8** : 404.

Carapus puntatus, Smith (J. L. B.), 1949, *Sea Fishes of Southern Africa* : 359.

Jordanicus punctatus, Smith (J. L. B.), 1955, *Ann. Mag. nat. Hist.* (12) **8** : 405.

Study material includes the type and nine other adults in the collection of the British Museum (Natural History); localities represented are Samoa, Pelew Islands, Tahiti. Varaii, Ovalau, Savaii and Wallis Island ; also one adult in the collection of the Universitetets Zoologiske Museum, Copenhagen, from Ghardaqa, Red Sea.

The type was obtained at Banda Island, Indonesia, and is now in the collection of the British Museum (Natural History) under catalogue no. 1861.2.28.51.

Specific characters. Greatest recorded length 236 mm.; length of head one-eighth to one-tenth or less of total length ; maximum depth of head about two-fifths of total length, maximum width slightly less ; horizontal diameter of eye equal to length of snout, slightly greater than interorbital width ; mouth almost horizontal ; jaw teeth well-separated from each other ; posterior part of lower jaw toothless in some specimens ; vomerine teeth one to four, in single median row, conical and of moderate size ; pectoral fins one-third length of head.

The colour of the living animal has been described upon four occasions, but the accounts are conflicting. Jordan and Evermann (1902) described a fish taken at Hilo as pale olivaceous with greenish spots. The colour pattern is given with meticulous detail, not only for the body, but also for the first and second dorsal, anal, caudal, pectoral and pelvic fins. Obviously, these notes do not refer to a fierasfer at all. The next description (Fowler, 1925) is of a specimen from the Natal Coast, recorded as " ecru-drab with darker mottlings", while in a subsequent paper (Fowler, 1926) the same specimen was described as pale mauve with a blue tinge. Smith (1955) described a specimen from Aldabra as translucent with a yellowish sheen and dark markings. The eggs and young stages of this species are unknown.

Measurements and proportions of representative adults are given in Table XVIII, and a summary for the specimens examined in Table XIX.

Table XVIII.—Encheliophis (Jordanicus) gracilis (*Bleeker*).

Measurements and Proportions of Adult Specimens.

Collection	British Museum.				Danish Museum.	
Number	1861.11.28.51.		1875.10.5.56.		—	
Locality	Banda.		Samoa.		Ghardaqa.	
	mm.		mm.		mm.	
Total length	116*		223		153	
Length of head	12·5	(11% TL)	23	(10% TL)	15	(10% TL)
Maximum depth of head	5·5	(44% HL)	10	(43% HL)	6	(40% HL)
Maximum width of head	5	(40% HL)	9	(39% HL)	5	(33% HL)
Length of snout	2·5	(20% HL)	4	(17% HL)	3	(20% HL)
Horizontal diameter of eye	2·5	(20% HL)	4	(17% HL)	3	(20% HL)
Vertical diameter of eye	2	(16% HL)	3·5	(15% HL)	2·5	(17% HL)
Interorbital width	2·5	(20% HL)	4	(17% HL)	3·5	(23% HL)
Length of maxilla	7	(56% HL)	10·5	(46% HL)	8	(53% HL)
Length of pectoral fin	4	(32% HL)	9	(39% HL)	5	(33% HL)
Maximum depth of body	6	(48% HL)	11	(48% HL)	9	(60% HL)
Preanal length	12	(10% TL)	21	(9% TL)	14	(9% TL)

* Type specimen.
TL = total length ; HL = length of head.

TABLE XIX.—Encheliophis (Jordanicus) gracilis (*Bleeker*). *Summary of Principal Measurements and Proportions of Adults Examined.*

Variate.	N.	R. mm.	M. mm.
Total length	11	116–223	178·2
Length of head	11	12·5–23	18·5
Depth of head	11	5·5–10	7·9
Width of head	10	5–9	6·9
Pectoral length	11	4–9	6·5
Preanal length	8	12–21	18·3
		%	%
Length of head (% TL)	11	9·6–11·8	10·4
Depth of head (% HL)	11	37·5–47·6	42·5
Width of head (% HL)	10	31·3–42·9	37·7
Pectoral length (% HL)	11	31·3–40·0	34·7
Preanal length (% TL)	8	9·1–11·8	9·8

N = number of specimens ; R = range of variate ; M = mean value of variate ; TL = total length ; HL = length of head.

This species occurs in the Pacific and Indian Oceans and has been recorded from Celebes, Indonesia, New Guinea, Cocos Islands, Pelew Islands, Fiji, Samoa, Tonga, Hawaii, Solomon Islands, Mozambique, Natal and Aldabra. The Pacific Ocean specimens have been found mainly in the starfish *Culcita discoidea*, while the specimen taken at Mozambique was in *Holothuria scabra.*

Fierasfer umbratilis has long been accepted as a synonym of *E. gracilis* and *F. frantii* has recently also been attributed to this species (de Beaufort & Chapman, 1951), since there is nothing in the very careful description to enable the two to be separated. The species long ago recorded from Mozambique as *F. punctatus* must belong to *Encheliophis* for its large size shows that it was adult, yet the teeth of jaws and palatines were in single rows only. A fierasfer in the Danish collection, obtained at Ghardaqa, Red Sea, is clearly referable to *F. neglectus* yet does not differ sufficiently from the available specimens of *E. gracilis* to be regarded as specifically distinct.

Encheliophis (Jordanicus) sagamianus (Tanaka), 1908

Carapus sagamianus Tanaka, 1908, *Annot. zool. jap.* **7** : 40. Tanaka, 1911, *Figures and Descriptions of the Fishes of Japan* : 25. Tanaka, 1927, in *Figuraro de Japanaj Bestoj*. Yosii, 1928. *Annot. zool. jap.* **11** : 339.

Carapus sagamius, Franz, 1910, *Abhandl. Bayer. Akad. Wiss. Suppl.* **4** : 31.

Jordanicus sagamianus, Matsubara, 1953, *Jap. J. Ichthyol.* **3** : 30.

The type was found in a holothurian taken in Sagami Bay, Japan, and placed in the Zoological Museum of the Imperial Science College, Tokyo, no. 1751. No specimens have been available for study and the following description is based upon those published by Tanaka.

SPECIFIC CHARACTERS. Greatest recorded length 190 mm.; length of head one-tenth of total length ; depth of head slightly greater than width ; horizontal diameter of eye equal to length of snout and to interorbital width ; mouth nearly horizontal; maxilla extends only to posterior edge of orbit; vomerine teeth in narrow band of four rows; pectoral fins one-third length of head; colour in life unknown.

E. sagamianus has been recorded only from Japan, at Sagami, Boshuu, Urugu and Misaki. It has been taken in the intestine of *Holothuria monacaria* and once in the starfish *Nardoa semiregularis* var. *japonica*.

Smith (1955) includes this species in the synonomy of *Encheliophis gracilis*, but gives no reason why the two species should be united.

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PART 1

INTRODUCTION

THE Zosteropidae (White-eyes) are a tropical passerine family, with a range over the whole of the Ethiopian Region and eastwards, through the islands of the Indian Ocean and India to Japan, the central Pacific and Australasia. There is, however, a gap of over a thousand miles, presumably imposed by ecological conditions, between about 50° E. and 66° E., across eastern Arabia, Persia and Baluchistan.

The family is for the most part very homogeneous, and has long been recognized as presenting special difficulties for the taxonomist. Stresemann (1931, 1939) has reviewed the populations from India eastwards, comprising about 180 forms, most of which are unquestionably to be placed in the genus *Zosterops*. For the remaining Zosteropidae, those of Africa and the Indian Ocean, no conspectus is available except the list incidental to the *Systema Avium Aethiopicarum* of Sclater (1930). He provisionally accepted 57 forms in the area and grouped them in 18 species of *Zosterops* (10 of them monotypic), 4 monotypic species of *Speirops* and 3 of *Malacirops*. In footnotes he mentioned 15 forms as probable synonyms ; and since he wrote 15 more forms have been described. More recently van Someren (1939), Grant and Mackworth-Praed (1943) and Mackworth-Praed and Grant (1945–46) have reviewed sections of the African continental birds, Bannerman (1948) has dealt incidentally with the West African forms, and Chapin (1954) with those found in the Belgian Congo. Between the various authors named there is great diversity of opinion about the number of forms that should be recognized and about their grouping into species. For example, of the 11 forms common to the discussions of both Chapin and Grant & Mackworth-Praed, Chapin admitted 4 that the other authors synonymized and differed from them about the specific allocation of 3 others. Agreement on local variation (at the subspecific level) is made more difficult because, as I believe, changes are liable to take place in the yellows and greens of *Zosterops* skins in a short time (see examples in Note 1 of Appendix 1). It may be added that most of the information about the biology of Zosteropidae is merely casual and incidental.

This study began as an attempt to revise the classification of the African Zosteropidae but as the work progressed I became increasingly impressed with the problems of their variation (as distinct from nomenclature) and their correlation with environmental factors. The opportunities for investigating these correlations are particularly good because Africa is so mountainous and otherwise provides so great a variety of habitats through which the *Zosterops* range.

Taxonomically, the great difficulty in this family is to determine the limits of the species. The *Zosterops* of Africa have more than once been cited as providing special problems when the concepts of allopatry and sympatry are applied. Lowland forms surround highland forms in such a way that their geographical ranges overlap in some cases completely, but their ecological ranges little if at all. In such cases the spatial barrier is, at most, of the smallest, a matter of a few hundred yards.

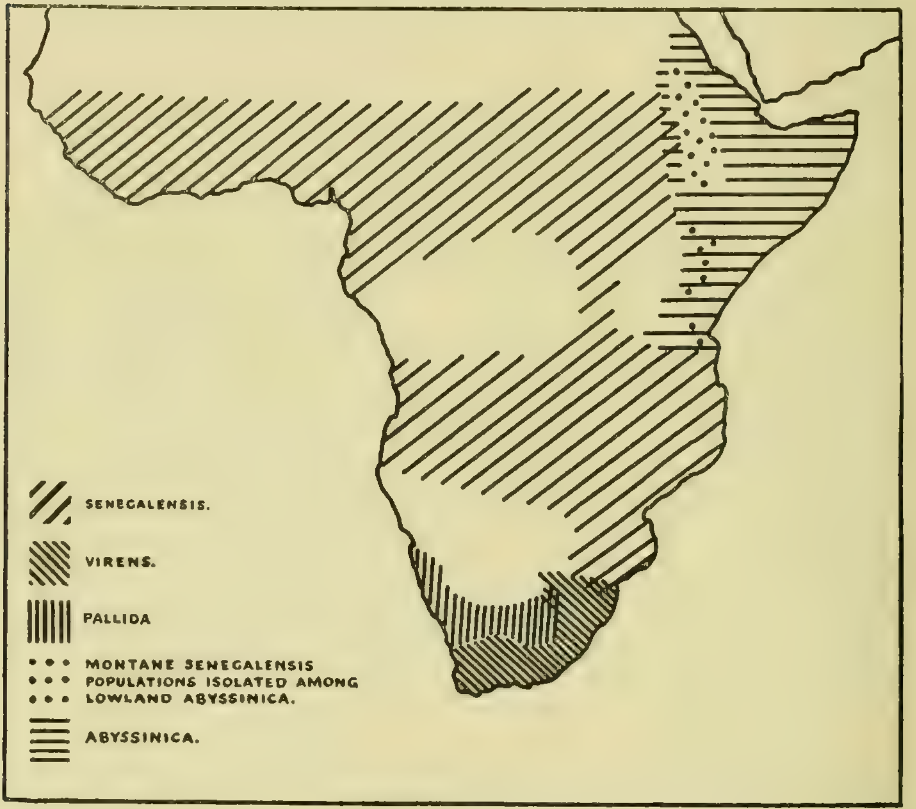
and cases (detailed in the appropriate sections below) have come to light in which, at least locally and temporarily, none exists. How far the breeding-seasons of the highland and lowland forms overlap in any one locality is unfortunately not known for any except the special case of Nyasaland (where they do—Benson, 1953). But on the whole it appears that where two *Zosterops* occur in Africa in the same small area, while they may be " genetically sympatric " (Cain, 1954) only marginally, they cannot be regarded as " genetically allopatric " to such an extent as to exclude the possibility of frequent interbreeding. In such circumstances, the absence or rarity of hybrids, whether of the primary type (evenly intergrading) or the secondary type (widely and sporadically variable), can be taken to mean that the forms concerned are genetically so incompatible that they are best treated as belonging to different species.

The subject of the present study is difficult to expound, partly because of the unavoidable amount of geographical and other detail, but also because of the difficulties inseparable from the use of trinomial nomenclature, which have been discussed by several recent workers (for example, Lack, 1946 ; Ellerman *et al.*, 1953 ; Wilson and Brown, 1953 ; Sibley, 1954). Nobody dealing with a large body of material from a continental area can fail to be impressed by the virtual impossibility of allocating every population, let alone every specimen, to a recognizable subspecies ; and if one is forced to attempt it for purposes of a check list it can only be at the cost of obscuring biological realities. An excellent example from the area under review is provided by the *Zosterops* of Madagascar. Originally they were treated as all belonging to one form ; now the palest birds and the largest birds have been separately named, though it has to be conceded that most of the *Zosterops* on the island are intermediate between the three subspecific types. I personally am deeply impressed not only with the shortcomings of the trinomial system but also by the harm that has been done to ornithology by the extremes to which the naming of local populations has been carried. Nevertheless, I regard the retention of some trinomials as essential, at least as a clerical convenience, especially when dealing with birds of a continental area. This is the spirit in which the trinomial is used in the present study.

In the pages that follow I shall first discuss the probable taxonomic significance of colour, which has hitherto been the sole character on which the specific classification of the Zosteropidae of Africa and the neighbouring islands has been based, and then the correlations of dimensions with each other and with environmental factors. This will bring into prominence certain basic principles, will show the extent of local variation and adaptation, and will lead to the conclusion that here dimensional characters can be only exceptionally and to a minor extent an aid to classification.

As regards classification at the specific level, I believe that reliance on colour characters has led to misleading results in the past ; and that some of the birds which differ conspicuously to the eye are more closely related than some of those which are most alike. In several islands on both sides of Africa two fully sympatric species of Zosteropidae occur—doubtless as a result of double invasion. By contrast, throughout the continent of Africa there are only two places, the upper slopes of

Cameroon Mt. and the south-western Transvaal, where two different forms are fully sympatric. In a third area, Zululand and its neighbourhood, two forms interdigitate, separated ecologically and apparently interbreeding little, while throughout north-eastern Africa a series of lowland forms, which I believe to form one polytypic species, surrounds a galaxy of isolated and well-differentiated montane populations. Besides the aberrant bird on the top of Cameroon Mt. which I keep in the genus *Speirops* (see discussion in Part 5) I provisionally group the African *Zosterops* as shown in Map 1:


SENEGALENSIS.
VIRENS.
PALLIDA
MONTANE SENEGALENSIS POPULATIONS ISOLATED AMONG LOWLAND ABYSSINICA.
ABYSSINICA.

Map 1. The ranges of *Zosterops* species.

Z. pallida, monotypic in south-western Africa and overlapping—
Z. virens, occupying the rest of South Africa and interdigitating with—
Z. senegalensis, a highly polytypic species occupying most of tropical Africa and becoming purely montane in the northeast, where it is surrounded by—
Z. abyssinica, a polytypic species characteristic of the dry lowlands.

These conclusions depend on a number of decisions that are by no means easy to take and the evidence needs to be set out in some detail (Part 4).

Following the description of the continental position, the insular populations on the opposite sides of Africa will be described. One special point of interest here is the evidence for double invasion, into one island after another, the evolutionary consequences of which can be fully appreciated only in the light of the continental situation. Further, the lines on which evolution has taken place in the Atlantic islands (Gulf of Guinea) have differed strikingly from those in the Indian Ocean Islands.

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SOME CHARACTERS OF THE ZOSTEROPIDAE AND OF THE AFRICAN MEMBERS

In appearance the Zosteropidae are rather " ordinary " passerines nearly all less than 14 cm. long. The size range is not great ; omitting two aberrant insular forms usually kept in the genus *Speirops*, within the present area the following are the extreme measurements : wings 49–69 mm., tails 30–53, beaks 11–17. Morphological characteristics of the family are absence or extreme reduction of the outermost primary, a fimbriated bifid tongue and a ring of silky-white feathers round the eye. The Zosteropidae are all short-winged birds, of direct flight, and thoroughly arboreal habits. The beak is rather sharp and slightly decurved.

Certain behaviour-characters of the family are significant in any consideration of their evolution :

(1) The birds have a wide range of food, taking fruit, insects and nectar, and in this respect there seems to be no specialization, local or other. Their feeding habits often bring them into association with sunbirds, alongside which they are always placed in taxonomic order.

(2) Individuals of most forms have a strong tendency to flock. Consequently birds journeying outside their normal area are likely to do so in groups and successful colonization is thus facilitated.

(3) White-eyes are liable to erupt and cross several hundred miles of sea. They have colonized more oceanic islands than any other passerine genus. That the Australian *Z. lateralis* invaded New Zealand across more than 1,000 miles of sea is a matter of history ; and that Norfolk Island, some 500 miles from any other *Zosterops* station, has been successfully colonized three times is certain from its three different forms of *Zosterops*.

(4) In conflict with this, the presence of highly differentiated populations on both marine islands and continental mountains within sight of each other seems evidence that the birds of some populations must be profoundly sedentary. An extreme instance is that of the *Z. rendovae* group (cf. Mayr 1947), where water-gaps of less than two miles separate subspecies.

Especially in a continental area, such as Africa, the birds would be expected to be most sedentary in the most equable environment (evergreen conditions) and least sedentary where the seasonal changes are greatest. There is good indirect evidence of this :

(*a*) A series of populations (52–54 in Appendix 3) having identical plumage and living in an evergreen-forest climate on the eastern rim of the Congo basin has average wing-length 61·3 mm. at 7,000 ft., 55·9 mm. forty miles to the west, at 4,300 ft., and 53·1 mm. twenty miles west again, at 3,000 ft.

(*b*) In East Africa very distinct populations live on forested mountains, separated from each other by as little as twenty miles.

(*c*) By contrast, the *Zosterops* ranging through the belt of deciduous thorn-bush south of the Sahara has not differentiated to the subspecific level in the three thousand miles from Senegal to the eastern Sudan.

There is little direct evidence of movement : the most definite is that the *Zosterops* characteristic of the very dry country of southern South West Africa sometimes appear for a few days in Windhoek (W. Hoesch *in litt.*), some 150 miles from where birds of this kind are known to be resident.

Birds usually assigned to the genus *Zosterops* comprise more than four-fifths of the Zosteropidae. Nearly all of these have the upper parts more or less green—

with a range of colour from dull pale grey-green to bright yellow-green and rich olive-green ; their throats and vents are more or less yellow. They have no distinctive patterns on wings or tails and no spots or speckles anywhere. There is no sexual dimorphism except that females tend to be a little smaller and, like juveniles, a little duller in plumage (having less carotenoid). Individual variation is, however, high—so much so that I should expect the results obtained by Marples (1945) to find a parallel in African populations if comparable series were examined. He was able to classify the belly-colour of *Z. lateralis*, trapped at Dunedin, New Zealand, in winter into nine different categories.

Apart from differences in shade and in dimensions, the main variations between populations are in three features :

(1) The width of the ring of white feathers round the eye (a feature that unfortunately does not lend itself to accurate measurement). Since an eye-ring exists in the vast majority of the Zosteropidae, and often is retained in aberrant forms whose other characters are much modified, it might be supposed to be of biological importance. But there is no evidence of its function, whether in display or in any other way, and within Africa it varies in extent from a conspicuous white patch, covering half the side of the head, to an almost imperceptible rim round the eye. Moreover it is sometimes altogether lost in otherwise " normal " *Zosterops*. On the whole it cannot be regarded as diagnostically useful except at the subspecific level.

(2) Markings on the forepart of the head. These are usually limited to lines above the lores and/or areas on the forehead where the melanin is reduced, so that they appear more yellow than the rest of the upper parts. If these brighter areas were sharply demarcated, they would be more comparable for taxonomic purposes.

(3) The underparts between the upper breast and the under tail-coverts. These are nearly always either yellow, with some green wash, especially on the flanks, or whitish washed with greyish or brownish. This feature is discussed specially in Part 2.

Particularly within the Zosteropidae discussed in this paper, there are extremely few clear-cut differences in pattern. Nearly all those perceptible between populations are merely a matter of degree—nuances of intensity of melanin or carotenoid ; while the one striking difference in pattern in the continental African birds, yellow or no yellow on the belly, which has been accepted as a specific difference, cannot be regarded as a reliable guide to relationships, as shown in Part 2.

Since the genus *Zosterops* includes over 200 recognized forms and for the most part varies only within the narrow limits indicated above, it is easy for widely separated populations to show resemblances that must be the result of convergent evolution rather than of close affinity ; and the systematist's task is correspondingly more difficult. For example Madagascar *Zosterops* are very like those of New Guinea (among others), those of the Australian mangroves (*lutea*) like those of the East African lowlands (*flavilateralis*), and those of Annobon Island in the Gulf of Guinea (*griseovirescens*) like those of Christmas Island in the Indian Ocean (*natalis*). Again, within our area, Madagascar *Zosterops* differ from those of south-western Abyssinia only in lacking golden foreheads and in having a little more melanin generally (characters that are not independent). Moreover, this difference is comparable to that (also confined to colour) between *Zosterops* from Madagascar and from India ; for, while most of the latter are much yellower than the former, Nilgiri birds are intermediate. Again, within Africa itself, some *Zosterops*, separated by hundreds of miles occupied by other forms, are indistinguishable, such as those of the mountains on the Sudan–Uganda border and some of those in Tanganyika Territory.

In such circumstances, where the appearance of the birds can be so unsafe a guide to their affinities, as many ancillary characters as possible must be considered. Among the most important of these is habitat preference. In his study of the eastern Zosteropidae Stresemann (1931) regarded their ecology (particularly their preference for lowland and highland habitats respectively) as an important guide to their relationships at the specific level. (Yet he was forced to postulate considerable change in ecological preferences in arriving at his grouping of forms into the polytypic *Z. citrinella* and still more in his enlarged concept of *Z. palpebrosa* (Stresemann, 1939)). There is no doubt that for African birds in general habitat preferences are highly specific, and in some cases generic, especially as between forest and non-forest and between highland and lowland habitats (cf. the analysis in Moreau, 1954). Unfortunately in the African *Zosterops* these distinctions and preferences are less clear-cut.

This is presumably due in part to their way of life : they are not ground-feeding birds, which in evergreen forests are immersed in a specialized eco-climate, nor forest-canopy birds, which may be limited by the distribution of certain species of fruiting trees or of tree-holes. Instead, the *Zosterops* have a wide range of diet and no specialized nesting-site ; moreover those forms which are attracted to evergreen forest appear to belong to the edges rather than the depths. (There is no *Zosterops* at all in the main Congo forest area, even in the clearings.) Also, most forms of *Zosterops*, including those of evergreen forest, seem to adapt themselves readily to whatever man-made conditions provide trees and associated food. Even those *Zosterops* which are always cited as forest birds, such as those in the southern Cameroons and on the East African mountains, may perhaps be looked upon as birds that use the arboreal associations dominating the locality rather than birds ineluctably dependent on forest, as most members of the evergreen-forest communities seem to be. If this view is correct, then different populations of the same species of *Zosterops* may be found occupying in one part of Africa savanna trees or even thorn-bush, and in others evergreen forest, with more or less ecotypical modification of characters. As will be pointed out, this is what happens in Madagascar, where *Zosterops* unquestionably of the same species occupy all types of vegetation and climate from the " subdesert " of the south-west to the east coast with over 100 inches of rain. Again, in South Africa birds that cannot be separated taxonomically are found breeding in a range of climate and natural vegetation from the coast of the Indian Ocean and associated evergreen forests, to the "high-veldt" of the Transvaal with its far greater daily and annual range of temperature and far drier and more deciduous "bush". This is not to deny that such birds as the montane *kikuyuensis* of the eastern Kenya highlands and the lowland *flavilateralis* are usually separated ecologically—even though in a marginal locality, such as near Nairobi, they may frequent the same garden. But it is at least clear that, in the key problem of which forms of the African *Zosterops* should be allocated to which species, in cases of difficulty the habitat preferences are not sure guides.

Other ancillary characters which have been considered are (1) colour of beak, iris and legs, (2) form of beak and tongue, (3) wing-formula, (4) voice, (5) feathering sequence of nestling. Certain of these, especially (2) are probably particularly adaptive and labile, but in any event, on examination, none of them seems to be capable of giving important clues in difficult cases. Details are therefore relegated to Appendix 2. Only two points in connection with them need be noted here :

(*a*) Such differences in wing-formula as exist seem to have neither taxonomic nor consistent ecological relationships. Two of the forms with the bluntest wings belong to dry country, but in two others of equally dry country (with open thorny trees) the character is not so marked ; and on other grounds there is little doubt that the four forms belong to at least three different species.

(*b*) Beaks and tongues are much alike in all the continental African and nearly all the insular birds under consideration, irrespective of habitat.

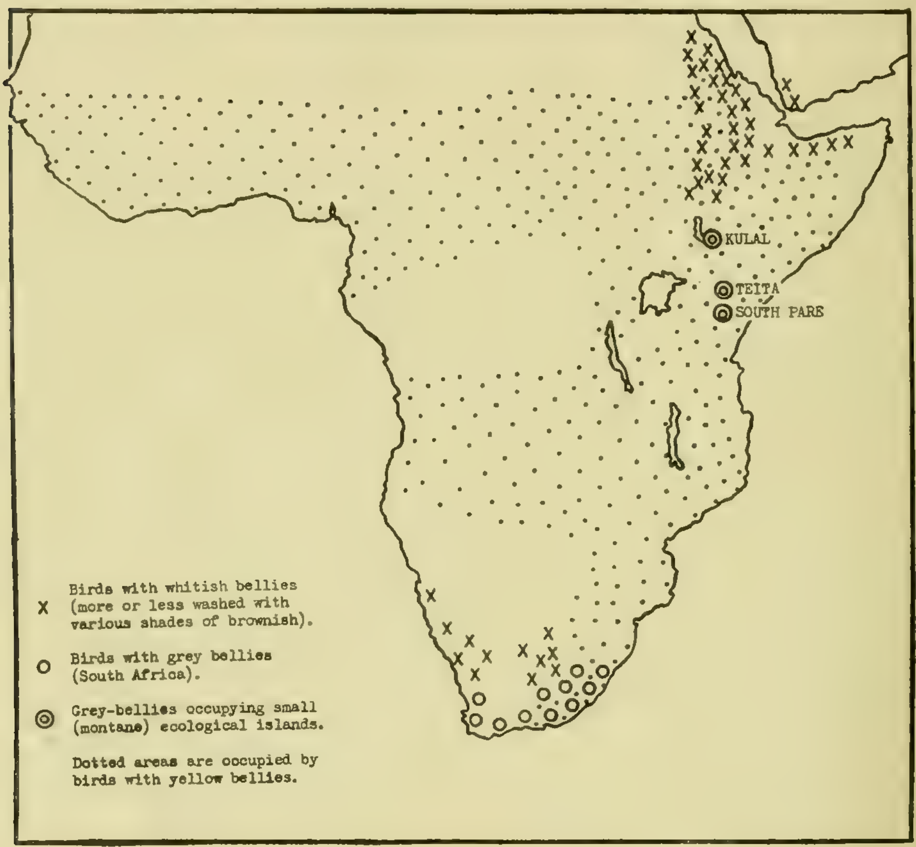
(*c*) The songs of some of the most different-looking African *Zosterops*, which have usually been allocated to different species, are apparently alike.

In attempting to discuss relationships and evolution one further difficulty is encountered, namely, apart from certain details of the plumage (see Part 2), there is no sure indication in the Zosteropidae of which features are the most readily modified. For example, *albogularis* of Norfolk Island has attained giant stature while retaining the presumed ancestral colouring, including full carotenoid and white eye-ring. Yet in a few forms the eye-ring seems to have been one of the first characters to be reduced or lost (at the subspecific level in *uropygialis* of one of the Kei Islands). On the other hand, one of the Seychelles birds, *modesta*, has lost all its yellow pigment, and become uniform grey, without becoming abnormal in size, proportions, beak or eye-ring. In the insular Zosteropidae, in fact, it seems that a rather limited variety of evolutionary changes can take place, with one exception, in almost any order.

PART 2

COLOUR, PATTERN, PIGMENT AND ENVIRONMENT

As indicated in Part 1, the most prominent colour differences between forms of Zosteropidae is that some have yellow pigment (more or less washed with green) on the belly and some do not. Stresemann (1931) noted in discussing the Indo-Pacific Zosteropidae that absence of yellow from the belly is much commoner than its absence from either the throat or the under tail-coverts. In fact, this last occurs only if yellow pigment is lacking from the whole of the rest of the underparts—which usually means from the upper parts as well. These generalizations apply equally to the African and insular Zosteropidae dealt with in the present study. It may be noted also that absence of yellow from the belly is unknown as an individual abnormality in a yellow-bellied population, though absence or reduction of carotenoid from the whole plumage occurs, as well as loss from defined asymmetrical patches (see Note 2, Appendix 1).


KULAL
TEITA
SOUTH PARE
X Birds with whitish bellies (more or less washed with various shades of brownish).
O Birds with grey bellies (South Africa).
◎ Grey-bellies occupying small (montane) ecological islands.
Dotted areas are occupied by birds with yellow bellies.

MAP 2. The geographical distribution of *Zosterops* belly-colour.

All who have dealt with the taxonomy of the African *Zosterops* have regarded the populations that have yellow bellies as specifically distinct from those which have not, though there has been no agreement about how many species of either type should be recognized. By contrast, however, in a number of polytypic Indo-Pacific

Zosterops species Stresemann (1931) and Mayr (1944) include both populations with yellow on the belly and populations without. Stresemann concluded that the difference probably depends on a single genetical factor. This must be true in any case where the two types co-exist and are proved to interbreed without producing any birds of intermediate plumage, but this condition does not seem to have been completely satisfied anywhere and at least in Java the evidence is against a single-factor explanation (Mees, 1951 ; Note 3, Appendix 1). There is in the island a complete range of variation between the yellow-bellied *gallio* and the grey-bellied *buxtoni* ; and it is instructive to note that many of the specimens are so like one of the parents that they would have escaped detection as hybrids if they had been seen in isolation.

In Africa what has been discovered in recent years about the relationship between the two types of *Zosterops* makes it virtually certain that here also belly-colour is not a specific character. For one thing, the grey-bellies occur only in widely separated areas (Map 2), isolated from each other by yellow-bellied populations that occupy equivalent niches in the intervening country (for details of distribution see Part 4).

The grey-belly locations fall into three groups :

North-east Africa.

In the Abyssinian highlands grey-bellied *poliogastra* and yellow-bellied *kaffensis* are almost allopatric and no intermediates are known.

The lowlands are occupied by grey-bellied birds (*abyssinica* and *omoensis*) except in the west-centre and the south-east. They are allopatric to yellow-bellied birds except near Lake Tana.

Kenya and Tanganyika Territory.

Here the numerous isolated mountains form an ecological archipelago. Grey-bellied *Zosterops* occupy exclusively (1) Kulal Mt. (*kulalensis*), (2) the Teita group (*silvana*), (3) the South Pare range (*winifredae*). The intervening and other mountains are occupied exclusively by various forms of yellow-bellied *Zosterops*, and each of the three grey-bellies is more like its nearest montane yellow-belly neighbour than any other.

South Africa.

In the Cape Province grey-bellies predominate in the west, yellow-bellies (otherwise identical) in the east. They overlap considerably and in the middle they are proved to interbreed commonly. Unfortunately the data do not suffice to settle the genetics.

Another form lacking yellow on the belly occupies South West Africa and overlaps the yellow-belly marginally, but in this case there is no evidence of interbreeding.

The foregoing data, taken as a whole, certainly suggest that in Africa colour of belly is a character with a simple genetical basis and that grey-bellied populations have developed repeatedly. In East Africa the montane grey-bellied forms have every appearance of having arisen as so many different mutants from the neighbouring yellow-bellies. It is concluded that in the *Zosterops* of Africa, as in those of the East, belly-colour is not necessarily a specific character. There is nothing to indicate how the present geographical pattern arose. It is difficult to believe that the character " grey-belly " is directly adaptive and, even with personal knowledge of East African mountains, I cannot suggest what factors can have operated particularly on Kulal, Teita and South Pare to select any characters with which " grey-belly " might be linked. It may be added that, though probably the Kulal and Teita birds are hardly to be numbered in thousands, the populations are far too big for the Sewall-Wright effect to be accepted as bringing about the present situation.

Much of the taxonomic discussion about the African continental Zosteropidae has turned upon the exact shade of yellowish green or greenish yellow of the upper parts, and the amount of green on the sides of yellow underparts. The colour intensity of the blackish lores and of the remiges and rectrices has also been adduced as a character. These are, however, not independent features because they are all correlated with the nature of the melanin present in the plumage as a whole and with the degree of its concentration. If much melanin is present in the upper parts, the yellow on the front of the head is, as a rule, less than in closely similar populations that have the upper parts as a whole not so dark. Conversely, the amount of greenish wash on the flanks generally varies with the darkness of the upper parts.

The physical basis of the coloration of the Zosteropidae does not seem to have been described anywhere and I am greatly indebted to Dr. L. Auber of the Wool Industries Research Station at Leeds for making microscopical investigations for me. It is hoped to extend and publish the results separately. Dr. Auber finds that in *Zosterops* pigments of only two groups are present, carotenoid (yellow) and melanin (three types). In the terminal (exposed) part of each contour feather the barb and/or the individual barbules have more or less of their length yellow and the rest melanic. Superimposed on each other in the plumage, they give, by a " lattice " effect, green. The exact shade depends on (*a*) the relative extension of the yellow and the melanized parts of each barbule, (*b*) the shade of each of the pigments, (*c*) their concentration and distribution within the tissue.[1] This last is especially important with the carotenoid, for the intensity of the yellow colour depends mainly on the thickness of the layer containing the pigment. This is especially important in the barbs, where the thicker the cortex (the layer holding the carotenoid) the more intense the yellow, towards golden or even orange. This effect appears to be mainly responsible for the striking difference between the pale yellow on the forehead of *abyssinica* and the strong reddish-golden of the Kenya *kikuyuensis*. In the former the unpigmented central core (medulla) of the barbs is wide, while in the latter it is so reduced that the barb forms practically a column saturated with carotenoid. Here, then, is a case in which the colour depends on the anatomy of the feather as well as on the pigment.

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[1] The conventional phrase " grey wash " or " green wash " is misleading in so far as it implies a pigment applied externally. In the *Zosterops* an impression of " grey wash " is given in an area of plumage that contains some melanin but little or no yellow pigment, and of " green wash " by an increase in melanization in the presence of yellow pigment.

With the melanins the optical effect depends largely, but by no means wholly, on the type of melanization. In approximate agreement with the observations of Görnitz (1923) and Frank (1939) on other groups of birds, Dr. Auber distinguishes three types of melanization in the African *Zosterops*, namely :

(A) Rodlets more than 1μ long, coated with blackish pigment and arranged with their axes parallel to the main axis of the barbule.

(B) Granules shorter and more irregular than (A) and which under the microscope look more brownish.

(C) Very small irregular granules, bright reddish brown. This type is rarer than the others in the African *Zosterops* ; it predominates (and causes a reddish colouring) only in the flank-feathers of the dry-country birds of south-western Africa (*pallida*) and in two insular birds (*semiflava* and *mayottensis*) living in a much damper oceanic climate.

Throughout Africa the melanin in the plumage of each form of *Zosterops* is predominantly or (usually) exclusively, of either (A) type or (B) type. Since the second pigment is much browner than the first it might be supposed that the type of melanization would proclaim itself to the eye but, for reasons not altogether clear, this is not always so. The outstanding example of this is afforded by the abnormal birds of the Gulf of Guinea islands, which are browner than any other Zosteropidae, yet contain much (A) type melanin. Again, the dry-country birds of rather dingy appearance in both north-east and south-west Africa, *abyssinica* and *pallida*, are dominated by (B) type, while the *Zosterops* of the humid São Tomé and Principe Islands, the upper parts of which look very similar, are filled with (A) type. Also, while in all the richer green *Zosterops* of Africa (A)-type melanization predominates, the Cape bird, which looks similar, is mainly (B) ; and such melanin as exists in the brightest yellow *Zosterops* in Africa, *senegalensis* of the dry belt south of the Sahara and *anderssoni* of the Rhodesias, is entirely (A). Incidentally, this explains the full blackness of the loral spot in these latter birds, a feature at first sight surprising in a *Zosterops* whose general plumage gives so little sign of black pigment.

In certain South African forms the proportion of (A) and (B) melanization in the individual varies with the humidity of the environment. Dr. Auber has found that in the birds of the western Cape Province (*capensis*) the admixture of (A) in the predominant (B) is greater in the humid Knysna area than in the arid Kamiesburg. Also, in *virens* of eastern South Africa the melanization is chiefly (A) in the humid Natal highlands, (B) in a dry-veldt habitat in the Transvaal. By contrast, *senegalensis* has all its melanin of (A) type, even in the driest environment (cf. a specimen from Maiduguri, near Lake Chad). This presumably means either that there is a different (undetected) environmental factor operating or, more probably, that *senegalensis* is physiologically (genetically) different from these South African birds and also from the other dry-country *Zosterops* (of north-eastern Africa), which are characterized by (B) melanin.

On the whole, as will be seen from the descriptions in Part 4, the more richly green birds throughout Africa occur in the more humid areas and this is everywhere linked—by whatever mechanism—with a greater intensity of (A) melanization in the plumage. There are very strong indications that the change takes place clinally in step with change in vegetation-type. The change is less closely correlated with total annual rainfall because other climatic factors, such as seasonal cloud-cover, extent of occult precipitation, and above all distribution of rainfall through the year, all determine the biological effectiveness of the rain. Thus, less than 60 inches of rain can suffice for evergreen forest if there is no long dry season, but not otherwise.

From all of the foregoing it will be evident that on the whole the African *Zosterops* conform to Gloger's rule, under which, as summarized by Mayr (1947), melanins increase in the warmer and more humid climates and in arid climates reddish- or yellowish-brown melanins increase at the expense of black. But in the African *Zosterops* it appears that melanins increase in the warmer climates only where the humidity is not reduced; and, so far as the type of melanin is concerned, the exclusive presence of black in the dry-country *senegalensis* is an exception to Gloger's rule.

To summarize this section, it appears that belly-colour cannot in these *Zosterops* be taken as a guide to taxonomic affinities, nor can general plumage-colour nor, as a rule, the type of melanization present—which often does not proclaim itself to the eye.

PART 3

DIMENSIONS AND THEIR CORRELATIONS IN CONTINENTAL *ZOSTEROPS*

The inquiry into these correlations was started in the hope of finding peculiarities and discontinuities that might help to elucidate the taxonomy of the birds. This section has taken its present form thanks to the statistical analysis arranged for by Mr. N. J. T. Bailey in his department of Design and Analysis of Scientific Experiment, at Oxford; and what follows here owes a great deal to discussions with him, with Mr. John Barlee and with Dr. H. W. Parker, who has devoted much time to the problems here raised.

The variations investigated are those of wing-length, tail-length and beak-length in relation to temperature and altitude, and in relation to each other. Investigation of these environmental effects is complicated by the fact that temperatures vary with altitude. Diverse as the temperatures are in different parts of Africa at the same altitude, in any given locality the temperature falls by about 3·5° F. for every 1,000-foot rise in altitude. The other factor that changes consistently with altitude, air-pressure, falls off by about 2·5%[1] of sea-level pressure for every 1,000 ft. of altitude and is not subject to important local variations.

By a suitable statistical technique the relations of dimensions to environmental temperature can be separated from altitude effects and considered independently, with special references to Bergmann's rule. As summarized by Mayr (1947), this is to the effect that " smaller geographic races of a species are found in the warmer parts of the range, the larger-sized races in the cooler ". Under " Rules applying to birds only " it is also stated that " the wings of races that live in a cold climate or in the high mountains are relatively longer than those of the races which live in the lowlands or in a warm climate ". It is not clear whether the word " relatively " means " relative to body-size "; if it does, then it must be noted that none of the references quoted by Mayr in support of this statement provide conclusive evidence.

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[1] This figure is net, taking account of the effect that the reduction in temperature has on the air-pressure. I am indebted to Dr. Parker for pointing out also that air-density is affected by humidity, being reduced as humidity increases; but the effect is small enough to be ignored for the present purpose.

Comparisons for this purpose have usually been made in the broadest terms, using latitude as an indicator of temperature, rather than actual meteorological data, and without discussing which elements of the environmental temperature are the most significant. It might be expected, *a priori*, that selection would be exercised by the more extreme conditions encountered ; Huxley (1942) in fact suggested that in the temperate zones these would be primarily the winter minima and in the sub-tropics (presumably even more in the tropics) the summer maxima.

The term used in the formulation of Bergmann's rule is " size ", which presumably means the size of the animal as a whole ; and consideration of the relations between size and temperature turns ultimately on the fact that, other things being equal, the heat exchange between a body and its environment depends on the ratio between its volume and its surface. The bigger and/or the more compact the body, the less rapid (per unit of mass) its heat-exchange. The bigger the body, the better it is fitted to withstand cold ; and the smaller the body the more easily it can, through radiation and evaporation, lose heat.

For vertebrates, weight is a useful indicator of size, but for most birds so little is known about the weight that in ornithology wing-length is almost always used as an index of body-size, with the tacit assumption that the relationship is linear. (Incidentally, the standard measurement of wing-length is not skeletal, but effectively that of the longest feather.) Now, if the shape of the wing and all the other bodily proportions remain constant, the " lift " provided by the wing varies as the square of the wing-length, while the mass of the whole bird varies as the cube. In these circumstances, if efficacy of flight is to be maintained it can be by an improvement in flying technique or by the length of the wing increasing faster than the linear dimensions of other parts of the body. In this case wing-length, so far from bearing a linear relation to the mass of a bird, would bear a complex and also continually changing relation to it, and hence to the bird's potentiality for heat-exchange.

Since no weights are recorded for African *Zosterops*, no data exist for testing the ratio of wing-length to mass in any of the populations[1], so that a link essential for any comprehensive discussion of size/temperature relationships is missing. Two further caveats are needed. The first is that the African *Zosterops* cannot all be claimed to belong to one species, which is a condition of Bergmann's rule ; but, as will be concluded, most of them appear to be conspecific. The other caveat is that heat-exchange depends on insulation as well as on mass and configuration ; we have no precise information on this point. It can only be said that the *Zosterops* of the higher, cooler, environments appear to have thicker plumage than the others.

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[1] An investigation of the mean weight of bird populations for statistical purposes such as the present would need especially long and critically collected series because the weight of the individual fluctuates so much with the time of day and season of the year. In *Zosterops* at Dunedin, N.Z., Marples (1945) found that *mean* weights of samples trapped on different days in the course of the year varied between 12 and 15 gm.

The dimensional data

For the present study about 2,500 specimens have been measured, a large proportion of all those housed in the museums of the world. As will be seen from Appendix 3, there are eighty continental populations of which enough specimens have been examined to give results useful for statistical treatment. Some of these " populations " coincide with named forms, but many of them do not. The latter are of three types : (*a*) geographical sections of forms with very extensive ranges, for example the respective Northern Rhodesian, Southern Rhodesian, Nyasaland and S.W. Belgian Congo populations of *anderssoni* ; (*b*) altitudinal divisions, as between the *Zosterops* of the eastern Kenya highlands above and below 9,500 ft ; (*c*) populations that are transitional and/or were not known to earlier workers (so that no subspecific name has been applied to them in the past). Other specimens and their dimensions are mentioned in the text as necessary.

All the measurements given in Appendix 3 were made by me personally, so that any subjective error should be fairly constant. Wings have been flattened and straightened, so that the measurement recorded is the greatest possible. Tails have been measured with one point of the dividers pressed down between the two middle feathers. Beak measurements are particularly difficult in *Zosterops* because of the lack of abruptness in transition from culmen to skull. At first, indeed, I felt that this measurement could not usefully be made, but eventually I found that fairly satisfactory results were possible—cf. the length-ranges in Appendix 3. In each case the point of the dividers was slid with gentle pressure up beyond the base of the culmen until it was decisively checked.

In the entire series of continental birds examined wing-length varies from 49 to 69 mm. in individuals and from 51·3 to 64 mm. in means. Extreme variation within populations is nearly always 4–7 mm., i.e. up to about 12% of the mean. The few populations in which it is much greater are either represented by exceptionally long series or could possibly be sub-divided if more specimens, suitably distributed geographically or altitudinally, were available. An example is provided in the highlands west of Lake Edward (populations 48 and 49 in Appendix 3). The specimens at first examined showed within this small area wing-lengths with the exceptional range of 54–65 mm. Later it was found that 31 birds from an average altitude of 4,700 ft. (the highest 5,000 ft.) measured 54–60 mm. and 10 from an average altitude of 6,800 ft. 58–65 mm. In general, individual variation in tail-lengths and beak-lengths is proportionately greater than in wing-lengths, perhaps partly because of the greater difficulty in making the measurements.

A small source of bias in the figures for the means comes from the fact that males, females and unsexed birds have all been used, provided that they showed no immaturity and no moult in the feathers to be measured. It would have been more satisfactory to use birds of only one sex, but this was rejected for two reasons. Firstly, the sexing of collected specimens is not always reliable and in some populations specimens that are not sexed form a large part of the material available. Secondly, although females are on the average smaller than males in most populations, the difference does not exceed 2 mm. in even the biggest *Zosterops*. Moreover, in nearly all the populations the proportion of sexed female specimens varies only between one quarter and one half of the total, and within these limits the most the mean could be biassed by this variable is about 0·5 mm. This is not enough to invalidate the general conclusions to be drawn later.

The meteorological data

For each population in Appendix 3 a mean altitude has been calculated for the specimens actually measured. (This mean does not necessarily agree with the mean altitude of the habitat of the *Zosterops* population concerned over its whole range.) Where no altitude is specified on the label of a specimen it has been estimated from its locality and such knowledge of the topography as could be obtained. It is thought that most of the mean altitudes given in Appendix 3 are accurate to within 500 ft.

These mean altitudes have been used as the datum-lines for calculating the temperatures that are given for each population in Appendix 3, namely, the mean minimum of the three coldest months and the mean maximum of the three hottest. (From these figures approximate annual means and annual ranges can be calculated as needed.) Thanks to the assistance of the Meteorological Office, Air Ministry, and supplementary information from African meteorological services, temperature data have been assembled for about 1,000 stations south of the Sahara. Within the geographical range of most of the populations in Appendix 3 a number of temperature records are available, some of the stations being as a rule higher and some lower than the mean altitude of the specimens concerned. From these records mean temperatures have been calculated and also the mean altitude of the stations. Where this differs from the mean altitude of the specimens available an adjustment has been made at the rate of 3·5° F. per 1,000 ft. Extrapolation has been used in two types of case :

(*a*) Where, as in birds from high altitudes in eastern Kenya and Mt. Cameroon, mean altitude of the specimens is thousands of feet above that of the local meteorological stations, the same factor of 3·5° F. per 1,000 ft. has been used.

(*b*) Where, as in the case of populations very narrowly localized, e.g. on single isolated peaks, meteorological stations are available only elsewhere in the same general area, a mean has been calculated from the data of the nearest ecologically comparable stations (and then the altitude correction applied if necessary).

Especially in the latter type of case, unknown local meteorological factors may invalidate to some extent such extrapolation, as personal experience of East Africa suggests, and for two of the populations in Appendix 3 I have thought it undesirable to attempt extrapolation. I am aware that some of the temperature means arrived at are open to criticism ; but all have been calculated as objectively as possible and the correlations that are about to be described show that in general the methods employed are valid.

WING-LENGTH IN RELATION TO ALTITUDE (AIR-PRESSURE) AND TEMPERATURE

In Text-figs. 1-3 the mean wing-lengths detailed in Appendix 3 are plotted respectively against altitude, minimum temperature and maximum temperature (as defined previously). In some respects these diagrams are illuminating, but they can, as will be shown, also be thoroughly misleading, for the reason that the three environmental factors are not independent.

In order to separate the effects of altitude and temperature, partial regression coefficients have been calculated, which give a measure of the influence that each

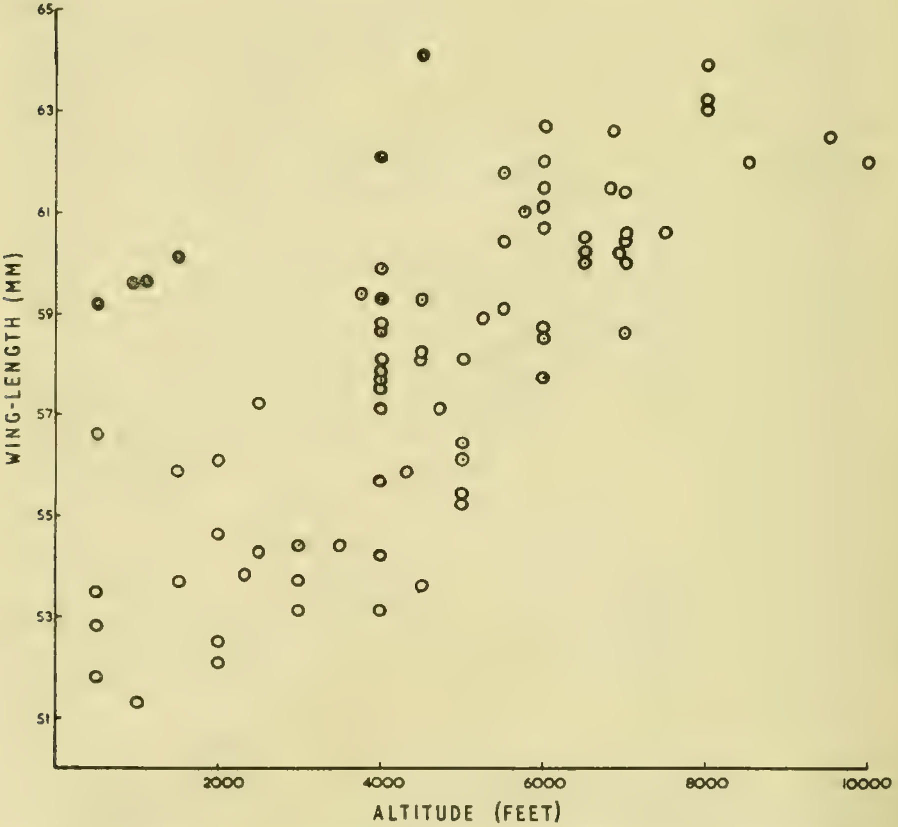

FIG. 1. Wing-length/altitude correlations. (Black circles, South African populations; dotted circles southern tropical.)

factor would have if it varied while the others remained constant. If w = wing-length (in mm.), a = altitude (in thousands of feet), n = minimum temperature (°F.) and x = maximum (°F.) the partial regression equation is :

$$w = 59{\cdot}8 + 0{\cdot}69a - 0{\cdot}28n + 0{\cdot}12x.$$

Each of these regression coefficients is highly significant statistically, since their standard errors are only 0·13, 0·04 and 0·05 respectively. It is to be noted, however, that each cofficient represents an average, and the data do not suffice for an investigation of whether the relationship in each case is rectilinear or not. From the purely statistical point of view the equation fits the observed data so closely as to warrant the conclusion that no environmental factor having a comparable

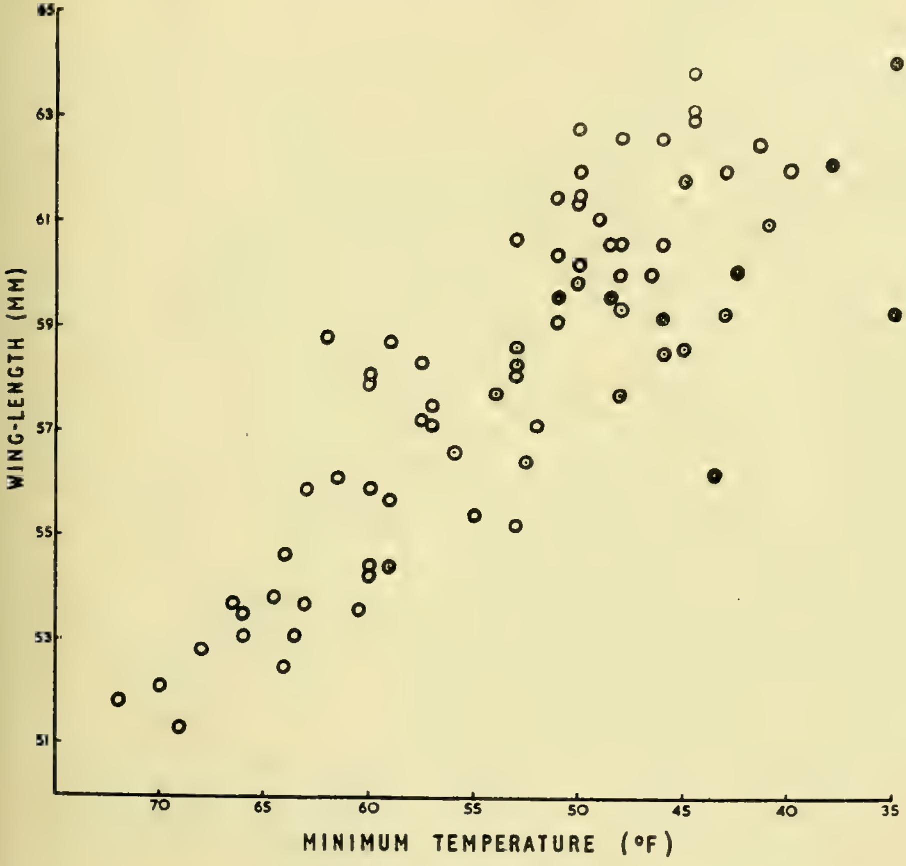

FIG. 2. Wing-length/minima correlations.

effect on the wing-length remains unconsidered. From the biological point of view this is in at least one respect questionable, as will appear.

Meanwhile, subject to these comments, it is concluded from the equation that on the average, over Africa as a whole :

(1) *Zosterops* wings tend to increase 0·69 mm. for every 1,000 ft. of altitude. Since the altitude range of the combined *Zosterops* habitats is 10,000 ft., the total potential effect of this factor is about 7 mm. (12% of the overall mean wing-length).

(2) *Zosterops* wings tend to decrease 2·8 mm. for each rise of 10° F. in the minimum. With extremes of mean minima 35° and 72° F. (Appendix 3), the total potential effect is about 10 mm. (17% of the overall mean wing-length).

(3) *Zosterops* wings tend to increase in length by 1·2 mm. for each 10° F.

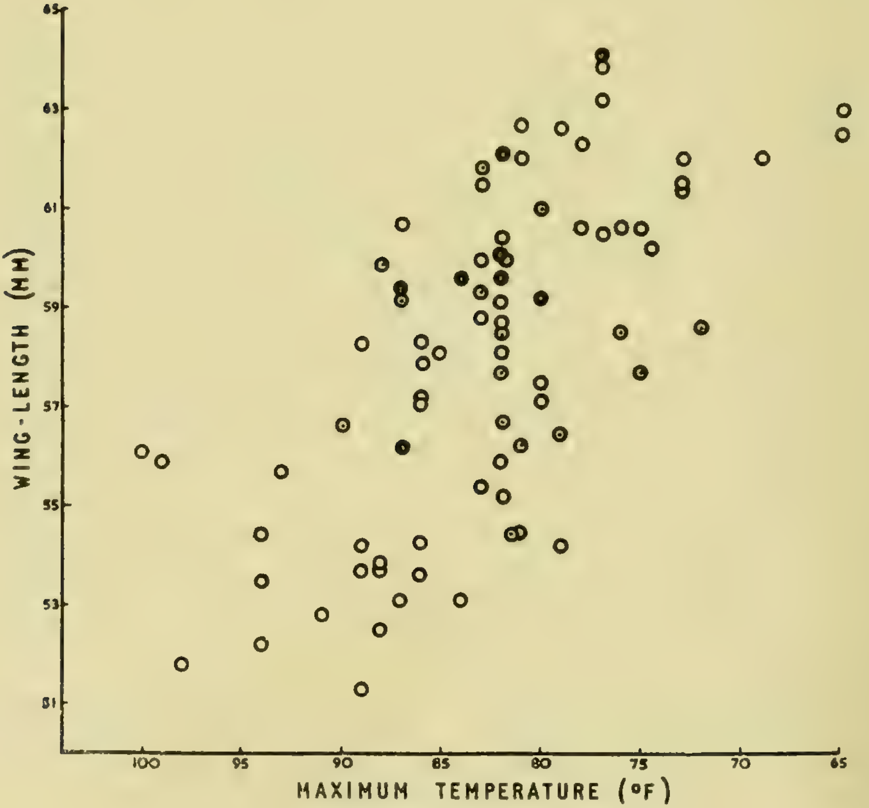

FIG. 3. Wing-length/maxima correlations.

rise in maximum temperature of the environment. Since the lowest maximum in Appendix 3 is 65° F. and the highest 100°, the total potential difference in wing-length attributable to this cause in Africa is only about 4 mm. (7% of the overall mean wing-length).

Wing-length and altitude

The equation shows that altitude has an important effect on wing-length that has nothing to do with temperature and hence presumably operates through the reduced air-pressure. No conclusive evidence of such an effect appears to have been presented hitherto for any type of bird. Long critical series of weights and wing-areas would be required for a closer examination of this phenomenon.

Since changes in air-pressure purport to be a direct cause of the changes in wing-length, then, when changes of pressure with altitude are plotted along with the changes in the " lift " provided by the wing, i.e w^2, the two " curves " might be expected to be of similar form. In fact they are not, because the pressure/altitude curve is very close to a straight line, while that of altitude/w^2 is quite different. The explanation may be complex. There is the purely statistical point that the addition of 0·69 mm. to the wing-length per 1,000 feet, is an average one ; as already noted, this may conceal a non-rectilinear relationship that the data are not " good " enough to disclose. Another, and strong, possibility is that the relationship between the wing-length and the mass of the bird is disturbed by various anatomical adjustments necessitated by changes in air-pressure. For example, in the species investigated by Norris and Williamson (1955) the ratio of heart-weight to total weight increased with the altitude at which the birds lived ; and similar changes in lung-capacity may be expected.

Text-fig. 1 shows that no population of small *Zosterops*, with wing averaging less than 58 mm., occurs above 5,000 ft. Another prominent feature of Fig. 1 is the grouping of the South African populations (black circles). Their appearance of being long-winged for their altitudes is undoubtedly due to the fact that South African temperatures are lower than those of tropical Africa at the same altitudes (cf. Appendix 3) ; it will be seen that this segregation of the South African points is not repeated when the wing-lengths are plotted against the minimum temperatures (Text-fig. 2).

It may also be noted in Text-fig. 1 that the populations of the highest altitudes, those of the upper levels of Mt. Kenya and of the Kivu volcanos, appear to consist of birds a little smaller than might have been expected. If this is genuine it might be a result of the following factors: (*a*) gene-flow, of necessity predominantly from lower altitudes, where the birds are smaller ; (*b*) marginal ecological conditions, implying poorer feeding—the hypothesis put forward by Davis (1938) to account for the unexpectedly small size of some mountain populations of rodents.

Wing-length and minimum temperature

The partial regression equation given above shows that wing-length increases as minimum temperature decreases—which is in accord with Bergmann's rule—and that this factor operates more powerfully than the others under consideration. Moreover, as shown by the consistent grouping of the points in Text-fig. 2 along an approximately straight line, this temperature factor (in conjunction with altitude) overrides any ecological adaptation, even though the populations involved occupy habitats as different as evergreen forest and dry thorn-bush. The consistency of the combined effect is further illustrated by the following facts extracted from Appendix 3 :

(1) Where populations otherwise similar are subjected to different minimum temperatures (and altitudes), those birds inhabiting the cooler climate have longer wings in 18 out of the 19 groups of comparable populations. (In these cases of course the altitude and minimum-temperature factors are reinforcing each other.) The only exception occurs in populations 59–64, and there the difference on the "wrong" side is extremely small.

(2) The five savanna populations on the south of the Sahara, nos. 14–18, range in wing-average only from 53·5 to 56·1 and the minima from 62° to 67° F. Yet even within these narrow limits the correlation is so effective that the populations with the shortest wings, 53·5 and 53·7, occur with the highest minimum temperatures, 66° and 67° F., and the other three wing-lengths are in inverse order of the temperatures.

(3) On the eastern rim of the Congo Basin, as already noted, on a line some 70 miles long from Kamituga eastwards (populations 52–54) mean wing-lengths fall from 61·4 mm. with minimum 50° (at 7,000 ft.) through 55·9 with 60° F. (at 4,300 ft.) to 53·1 mm. with 66° F. (at 3,000 ft.)—another case in which altitude and temperature are operating together.

The only local peculiarity disclosed by Text-fig. 2 is that the South African populations (black circles), grouped as they are to the right, have rather shorter wings than would be expected from the low minimum temperatures. Since among the African Zosteropidae they alone are outside the tropics, the first suspicion is that we have here a " latitude effect " such as Snow (1953) demonstrated in the Paridae. He suggested that in the short daylight of winter the high-latitude tits could not maintain a body of the size most efficient for heat-conservation. This could hardly apply to South African birds, the duration of whose feeding days in winter would be only 2–3 hours shorter than those on the equator—and much longer than those in the latitude of Britain ; but I can think of no acceptable ecological reason why South African *Zosterops* should show this peculiarity.

Among the South African birds two populations are outstanding, namely the *pallida* of the south-west and the (higher-altitude) *pallida* of the Orange Free State. Both have conspicuously shorter wings than might have been expected from the low minimum temperatures—which are well based on local meteorological records. This effect is the more remarkable because the maximum temperatures are rather high and hence favour lengthening of the wing.

In connection with this peculiarity of *pallida* two possibilities may be suggested. First, the bodies may be stunted as an adaptation to rigorous ecological conditions.

This seems unlikely because, although the environment of South West Africa, with its aridity and extreme daily range in temperature, is one of the harshest experienced by *Zosterops*, in the Orange Free State, especially along the Vaal River, whence some of the specimens come, conditions are not so bad. The alternative possibility is that in this *Zosterops* the wing is abnormally small for the body. No data exist for testing this : but these birds show another peculiarity that is presumably not independent, namely an extremely high ratio of tail-length to wing-length, as is obvious in Text-fig. 5.

Wing-length and maximum temperature

The statistical demonstration that the wings of African *Zosterops* tend to get longer as the maximum temperature rises is contrary to Bergmann's rule. It is also contrary to the impression given by Text-fig. 3, but this is undoubtedly fallacious and due to the fact that (as shown by the equation) minimum temperatures and altitude have, in combination, an effect on wing-length powerful enough completely to mask the influence of the maximum temperature. Here, then, in Text-fig. 3 we have an outstanding example of the misleading result that can be produced by the use of a graphical method unchecked by statistical analysis.

The tendency for wing-length to increase with a rise in the maximum temperature is difficult to explain on biological grounds, because the reverse would be expected. It should, however, first be pointed out that temperature is not an adequate index of the demands made by the environment on the bird's potentiality for heat exchange, because evaporation depends greatly also on the relative humidity of the air. This is subject to wide local variation according to the general climate and cannot be neglected when the effects of maximum temperatures on heat-exchange are being considered.[1] Far too few stations record relative humidities for it to be possible to calculate the mean saturation-deficits experienced in the hot season by any of the populations under discussion. All that can be said, from a knowledge of the climatic régimes, is that more of the very high maxima are accompanied by low humidities, and hence are biologically less exacting, than are accompanied by high humidities. And it is virtually certain that if the populations could be arranged in order of the saturation-deficits they experience in the hot season it would differ a good deal from that of their hot-season maximum temperatures.

In birds exposed to the greatest heat some special adaptations for escaping or reducing the full effect may be present—faster breathing with or without gaping, a higher ratio of surface (internal and/or external) to mass, thinner plumage, or a persistent seeking of the coolest available eco-climates.

Wing-length and other temperature combinations

It has been suggested that it might be interesting to ascertain whether statistically significant correlations exist between wing-length, annual mean temperature (*m*) and annual range in temperature (r), m being $\frac{\text{max.} + \text{min.}}{2}$ and r max. − min. The partial regression equation with altitude then becomes:

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[1] This does not apply to minimum temperatures, which are practically always accompanied by high humidities, if not by dew-fall.

$$w = 59{\cdot}8 + 0{\cdot}69a + 0{\cdot}20r - 0{\cdot}16m.$$

(Standard errors of both m and r are ·04, so that both coefficients are highly significant.) This means that wings tend to be shorter with higher means and to be longer with greater annual ranges. The effect of the higher mean would be in conformity with Bergmann's rule; and the effect of the higher annual range is what would have been expected from the first equation. For annual range is a reflection of both higher maxima and lower minima; and each of these factors was shown to be correlated with longer wings.

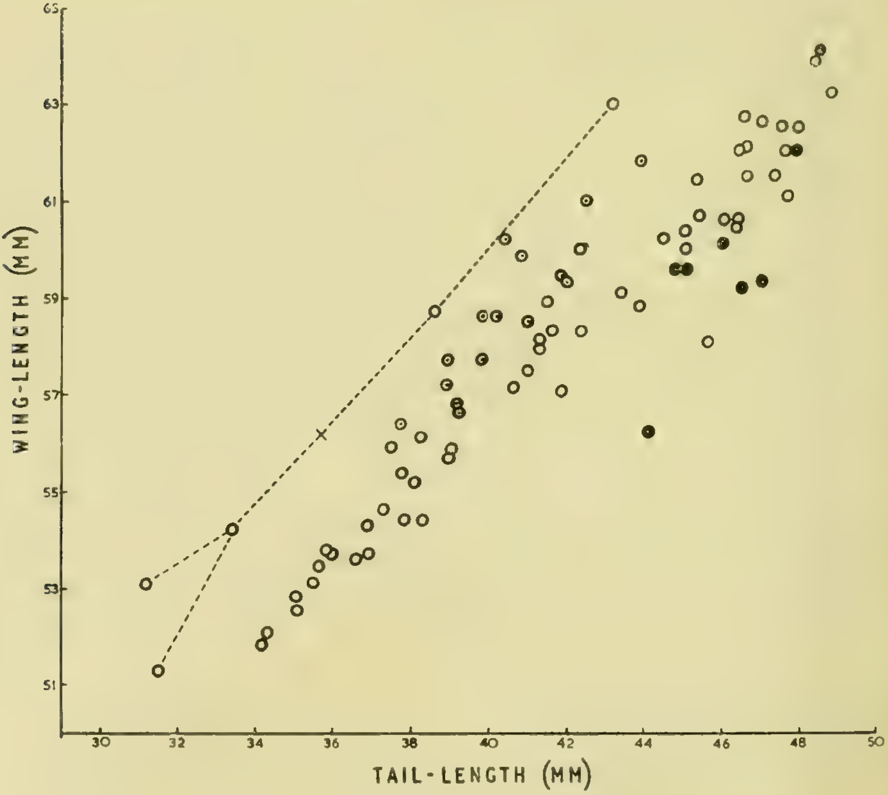

FIG. 4. Wing-length/tail-length correlations.

TAIL-LENGTH IN RELATION TO WING-LENGTH AND ENVIRONMENT

Mean tail-lengths vary from 31·2 to 48·7 mm. and the correlation between mean tail-length and mean wing-length is remarkably high, + 0·93—cf. the grouping in Text-fig. 4. Conformably, the equation showing the multiple regression of tail-length (t) on altitude, minimum temperature and maximum temperature takes exactly the same form as that of wing-length (p. 329), being :

$$t = 44{\cdot}0 + 0{\cdot}73a - 0{\cdot}44n + 0{\cdot}21x.$$

Again, these figures are highly significant statistically (standard errors 0·19, 0·05 and 0·07 respectively) and they mean that the tails tend to increase with altitude, with fall in minima and with rise in maxima. These effects can, however, be shown to be due almost entirely to the closeness of the correlations between wing-length

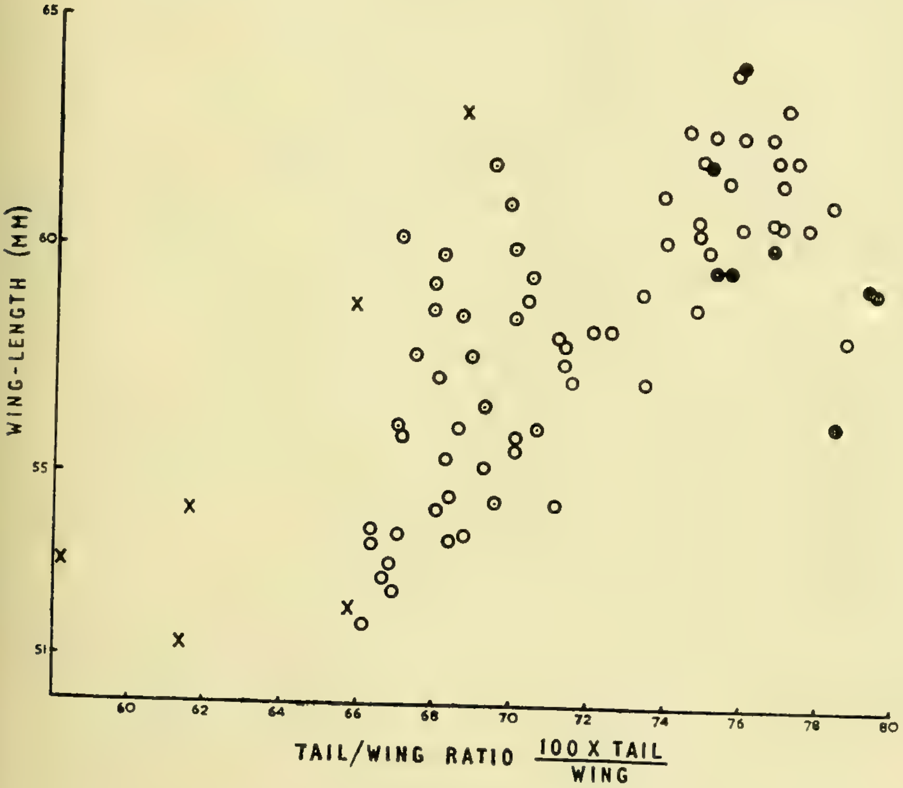

FIG. 5. Correlations between wing-length and tail/wing ratio.

and tail-length because, when the multiple regression of tail-length is calculated on wing-length together with the other factors, the equation becomes :

$$t = -30{\cdot}50 - 0{\cdot}120a - {\cdot}92n + 0{\cdot}062x + 1{\cdot}246w.$$

Of these the wing factor (w) is highly significant (standard error 0·114), the minimum temperature is just significant (standard error 0·45) and the others are not significant.

Reverting to the first of these two equations, and applying the same method as was used with the wings (p. 330), it can be inferred that in the African *Zosterops* the potential total effect of altitude on tail-length is 7 mm., of minimum temperature 15 mm., and of maximum temperature 7 mm. These figures, 17%, 37% and 17% respectively of the overall mean tail-length, are proportionately greater than the corresponding effects, 12%, 17% and 7%, of the respective factors on the wing. Hence, compared with the wing, the tail is relatively more sensitive to the effect of temperature than to that of altitude. This is confirmed by the last equation, in which it is shown that minimum temperature has a significant influence (along with wing-length) on tail-length, but that altitude has not. This result accords with the probability that variations in air-pressure may not exercize a strong and direct influence on tail-length ; and certainly not so strong as on wing-length.

As shown in Text-fig. 5, the tail/wing ratio rises with increasing wing-length ; in fact, even omitting the abnormal Cameroons group (marked × in Text-fig. 5), in the shortest-winged populations the tails average only about 67% of the length of the wings, while in the longest-winged tails average about 76%.[1] It is shown by the last equation that this is unlikely to be due to a direct altitude effect, i.e. to depend on air-pressure (cf. the scatter when tail/wing ratios are plotted against altitude in Text-fig. 6), but the possibility of a temperature effect is not excluded. Thus, the African *Zosterops* seem to show the same phenomenon as the Palaearctic Paridae, in which tails are proportionately longer in colder climates (Snow, 1953). It is possible that the same holds good in Malaysian birds generally (Longhurst, 1952), but the climatic data cited for these leave something to be desired. This result is terminologically at variance with Allen's rule, under which extremities are proportionately shorter in cooler climates ; but this rule is probably not applicable to an appendage such as a bird's tail, in which there is no circulation and the heat-exchange is presumably negligible.

The biological reason for the progressive change in the tail/wing ratio of the African *Zosterops* is difficult to suggest. I owe to Mr. Bernard Stonehouse the idea that if, as appears, the *Zosterops* inhabiting the cooler climates have more ample contour feathers, then the other feathers might share in the process of elongation ; and owing to the less specialized nature and function of the tail-feathers this process might in them be less subject to modification by natural selection than in the flight-feathers.

There are no marked discontinuities in Text-fig. 4 although two geographical groups occupy slightly aberrant positions. Moreover, in these two groups the alignment of the points is parallel to that of the main body. It can be concluded that the same principles are operating in all forms of *Zosterops* and that there is no overriding adaptation of tail/wing ratio to habitat (in particular, to open thorn-bush as against evergreen forest).

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[1] Since the above was written I have received Mees' paper in *Sarawak Mus. J.*, **6** (1955) : 641–661, in which he describes a similar change in tail/wing ratio with wing-length in certain eastern Zosteropidae.

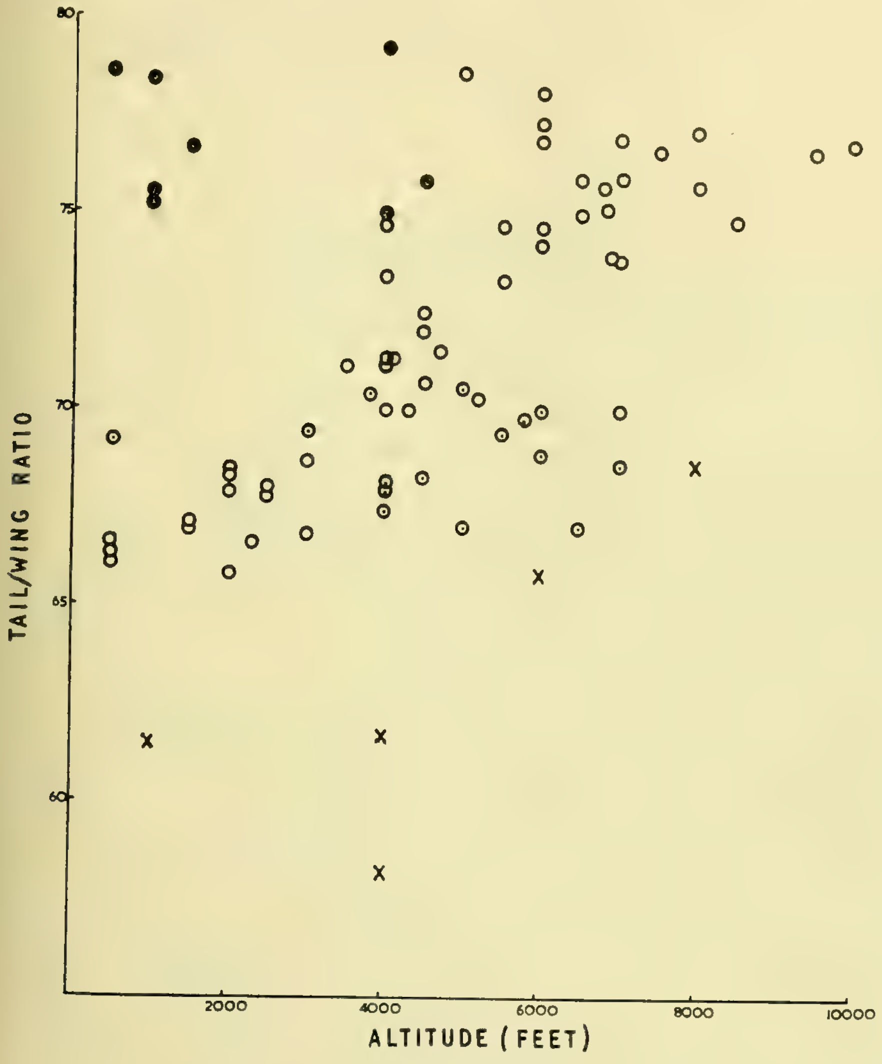


FIG. 6. Correlations between tail/wing ratio and altitude.

In Text-fig. 4 certain populations, 19–23 and 66 in Appendix 3, lie to the left (open circles joined by the broken line), that is, their tails are abnormally short in relation to their wings. The segregation of 19–23 is equally marked in Text-figs. 6 and 7, where tail/wing ratio is plotted against altitude and minima respectively. All the populations concerned lie round the head of the Gulf of Guinea on and near Cameroon Mt. (see Map 5), except 66, which is in Tanganyika. Moreover the tail/wing ratio of the birds of Fernando Po (× in Text-fig. 4), which are identical in plumage, lie on the same line exactly. The biggest bird in this series (wing 63 mm.), from the

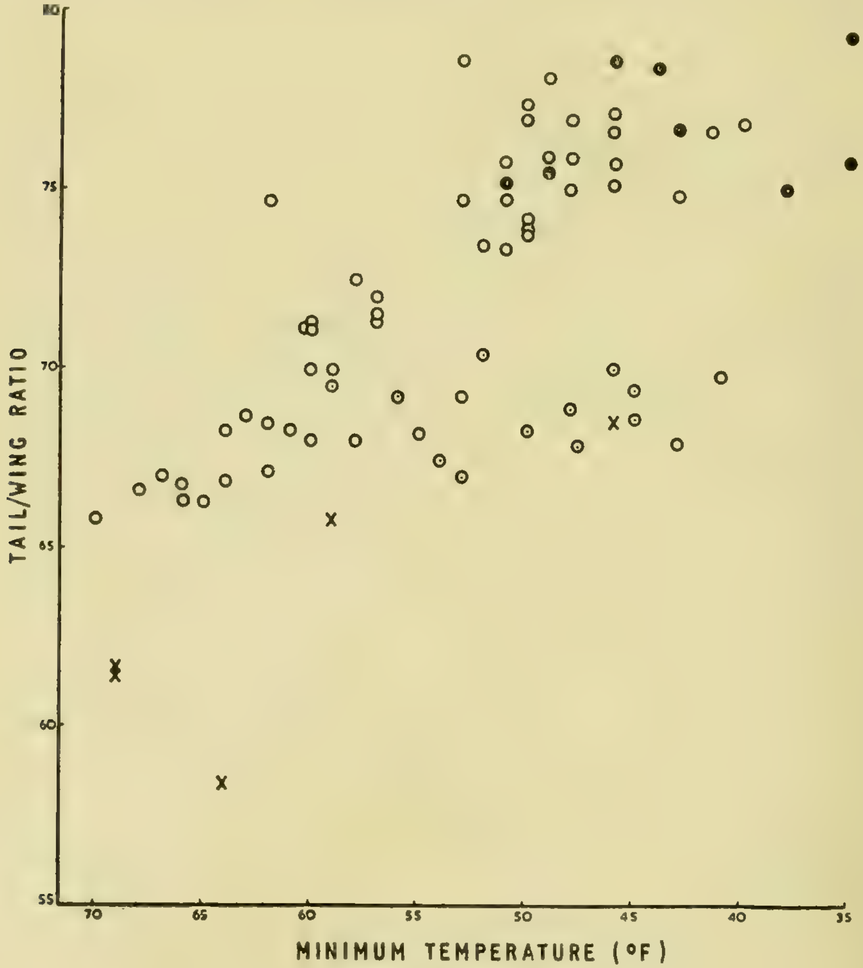


FIG. 7. Correlations between tail/wing ratio and minima.

top of Cameroon Mt., is so generally aberrant as to be placed in a different genus (*Speirops*), but nevertheless its tail/wing ratio is on the same, abnormal, line as those of its unrelated neighbours. This suggests that the character " short tail " in the other Gulf of Guinea birds may not be of taxonomic significance, but is related to some ecological peculiarity of the area.

The South African populations (usually attributed to at least two different species) are not completely separated in Text-fig. 4 (black circles) from the remainder, as are those of the Cameroons, but they do all lie to the right, having their tails abnormally long for their wings. It seems unlikely that this can be correlated with some peculiar environmental factor, because the birds concerned inhabit an extremely wide range of habitats (as described in Part 4).

BEAK-LENGTH IN RELATION TO WING-LENGTH AND ENVIRONMENT

Correlation between beak-length and wing-length is high, + 0·83. The partial regression equation for beak-length (*b*) on altitude, minimum and maximum temperatures is of the same pattern as those for wing and for tail, namely :

$$b = 14{\cdot}11 \text{ mm.} + 0{\cdot}144a - 0{\cdot}039n + 0{\cdot}005x.$$

In this equation a and n are significant, with standard errors 0·04 and 0·012 respectively, but x is not. Hence it is inferred that altitude and minimum temperature each affect beak-length, in the same way as they do wing-length, but to the same potential extent, each up to a total of 1·5 mm.

If now, as in the case of tails, the partial regression of beak-length is calculated on wing-length as well as on the environmental factors, the equation is :

$$b = + 0{\cdot}44 - 0{\cdot}013a + 0{\cdot}25n - 0{\cdot}022x + 0{\cdot}229w.$$

Again, the last factor, wing-length, is highly significant (standard error ·031), the minimum temperature just significant (standard error ·012) and the altitude and maximum temperature not significant. This means that the over-riding factor in determining the length of the beak is the length of the wing (i.e. presumably the general size of the bird), but that there is also a slight tendency for beak-length to increase with higher night temperatures. This would accord with Allen's rule, under which exposed, terminal, parts of the body are proportionately longer in warmer climates.

When beak-length is plotted against wing-length (Text-fig. 8), the data look homogeneous. Points relating to birds of dry country are not segregated from those of forest. Hence there is no important adaptation of beak-length to type of habitat or type of tree.

In Text-fig. 8 it will be seen that as a whole the southern tropical populations (distinguished by a dot in the circle), some of which live in savanna and some in mountain forest, have a beak-length that is nearly constant in spite of differences in wing-length. This is interesting because the populations comprising this southern group have usually been divided between two species.

With one exception, the *Speirops* of the top of Cameroon Mt., the beaks that are longest in relation to wings all belong to birds of the highlands of Abyssinia, eastern Kenya and north-eastern Tanganyika (squares on Text-fig. 8), a group of populations there are other grounds for thinking closely allied. In this respect (though the differences are very small) they stand apart from the *Zosterops* of the other high mountains of Central Africa and western Kenya. For this no ecological reason can be suggested, since all the mountains are characterized by evergreen forest and this is represented by the same type, though not exclusively, in both areas.

The two populations with proportionately the longest beaks of all are those (otherwise different in both dimensions and plumage) confined to the tops of the

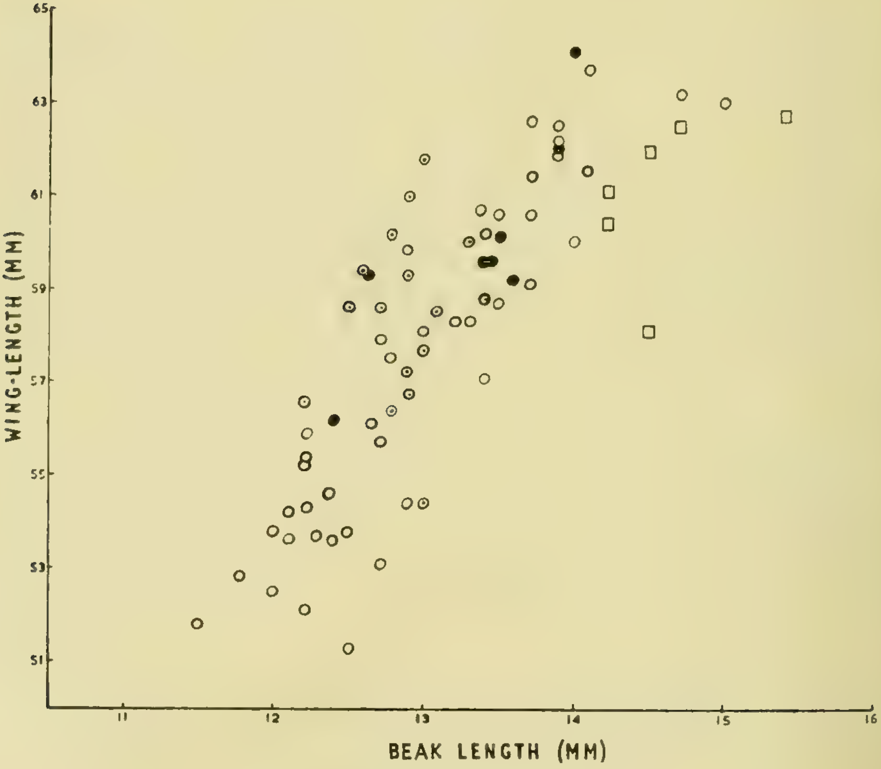


Fig. 8. Wing-length/beak correlations.

widely separated Kulal and Teita Mountains (populations 28 and 34 in Appendix 3). Again, no ecological reason can be suggested. The number of individuals on each mountain is certainly small, so that in this respect conditions are from the evolutionary point of view more comparable with that of a bird-population on an oceanic islet than of one living in a continent.

DIMENSIONAL CORRELATIONS AND TAXONOMY

The one bird of undoubted taxonomic distinctness at a high level, the *Speirops*, is abnormal in only one of these correlations, namely tail/wing ratio, and in that it agrees with its immediate neighbours.

On the other hand, there are four groups that show some peculiarity not explained on ecological grounds, which might therefore be regarded as primarily phylogenetic:—

South African birds (black circles in text-figs.). On the whole these are unusually long-winged (? large) for their altitudes and somewhat short-winged (? small) for their cold-season minima, especially in the case of *pallida*. They also tend to have high tail/wing ratios and they are segregated from other African *Zosterops* when this ratio is plotted against altitude (Text-fig. 6) and, less sharply, against minimum temperature (Text-fig. 7). In this respect also, *pallida* is the most divergent of the South African birds.

Southern tropical populations (dotted circles in text-figs.). These birds are geographically contiguous with the South African, but they differ markedly from them in their tail/wing ratios: the points in Text-fig. 5 are distributed in two parallel linear groups. This segregation is noticeable also when tail/wing ratios are plotted against altitude (Text-fig. 6) and against minima (Text-fig. 7). Also the southern tropical birds tend to have beaks of much the same length while their wing-length varies. These facts suggest that the southern tropical birds form a single species distinct from the South African birds.

Cameroons group (crosses in text-figs.). The tail/wing ratio is aberrant (Text-fig. 5) not only in itself but also in relation to altitude (Text-fig. 6) and minima (Text-fig. 7). But because this peculiarity is shared by the local *Speirops* it is thought not to be of taxonomic significance.

East and northeast African montane birds. The beak/wing ratio of these birds, commonly divided into several species, is consistently high.

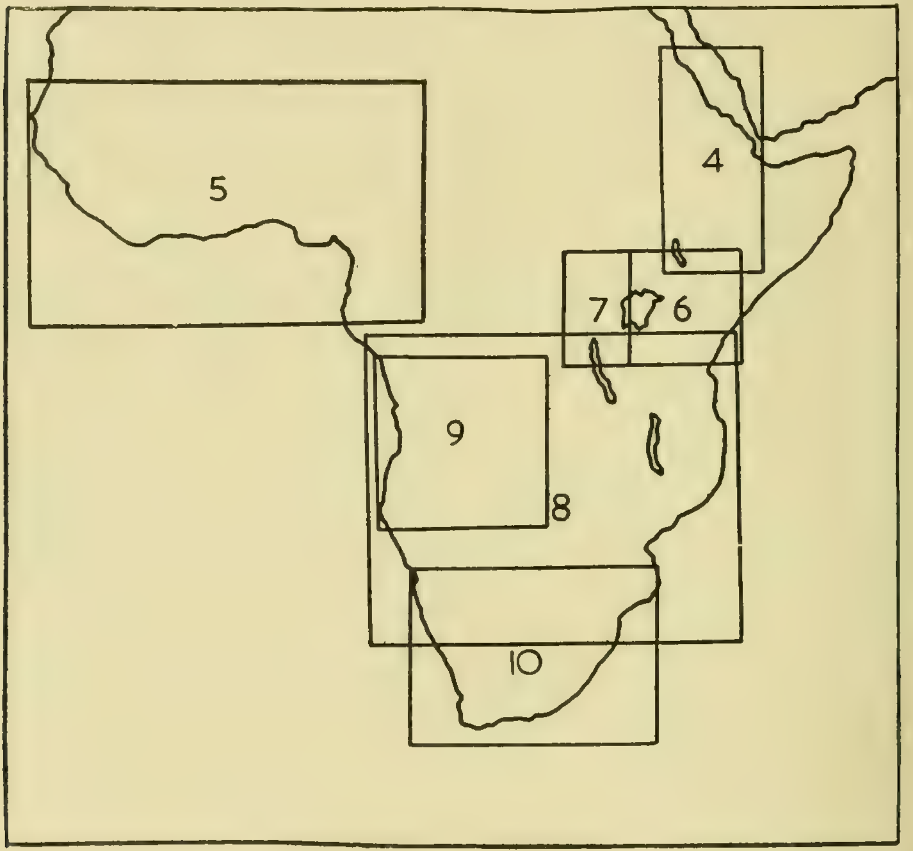
Conclusion. The foregoing analyses disclose correlations of dimensions with each other and with environmental factors that are remarkable for their general application throughout the continental African Zosteropidae. There are no abnormalities so striking as to provide compelling reasons for separating populations at the specific level, though peculiarities exist that may serve as ancillary characters, to be considered in cases of disputed relationships.

The dimensions of insular populations, which are given in supplementary tables in Appendix 3, do not lend themselves to statistical analysis on the same lines as the continental data. The results obtained above give, however, standards of comparison, utilized in Part 5.

PART 4

CONTINENTAL POPULATIONS: CHARACTERS AND INTERGRADATIONS

In this part the *Zosterops* of Africa will be described in six geographical sections (see Map 3 for key to local maps), an arrangement adopted in order to assist exposition of the complicated material. At the end of each section the main outlines will be summarized and the appropriate nomenclature indicated. The taxonomic arrangement at the specific level is discussed as a whole in the general synthesis (Part 6); meanwhile, the results have been anticipated in Part 1 and sketched in Map 1. Throughout the sections that follow, the discussion will be in the light of the correlations and general principles dealt with in Parts 2 and 3.



Map 3. Key to area maps.

NORTH-EAST AFRICA

Throughout Eritrea, Abyssinia and Somaliland the lowlands are dry, with acacias and combretums as the dominant trees ; and the east and southeast are particularly arid. The highlands still carry patches of evergreen forest, largely in its driest form (dominated by *Juniperus procera*), but richer in the more humid south-west of Abyssinia.

The *Zosterops* situation is most complicated and interpretation is hindered by the lack of field data. Six main forms exist, the habitats and chief characters of which are outlined in Table I. The last two (highland) forms have always been regarded as specifically distinct, both from each other and from the lowland forms. The latter conclusion is no doubt correct, the former probably not (see below).

TABLE I.—*Main Characters and Habitats of the* Zosterops *of N.E. Africa.*

Range.	Habitat.	Name used by Sclater (1930).	Colour of	
			Upper parts.	Belly.
N. and E., lower altitudes (up to 5,000 ft.)	Any arborescent vegetation (Erlanger 1907, K. D. Smith *in litt.*)	*abyssinica*	Grey-green	Greyish
S. E., lower altitudes (up to 6,000 ft.)	Dry acacia country (Erlanger 1907). Thorn scrub and, exceptionally, juniper woods (Benson 1946*b*)	*smithi*	Greyish yellow-green	Yellow
N.W., lower altitudes (up to 6,000 ft.)	" Steppe " (Neumann 1906)	*senegalensis*	Yellow-green	Yellow
S.E., lower altitudes (up to 6,000 ft.)	" River valleys " (*ibid.*) Deciduous forest (Cheesman *in litt.*)	*omoensis*	Yellow-green	Greyish
Western highlands (4,500–9,000 ft.)	Mountain forest (Neumann 1906)	*kaffensis*	Rich green	Yellow
Highlands elsewhere (5,000–10,500 ft.)	Evergreen forest (cf. Benson 1946*b*)	*poliogastra*	Rich green	Grey

The geographical distribution of the six forms is shown diagrammatically in Text-fig. 9. It will be seen that a grey-bellied and a yellow-bellied form divide the highlands between them, while round them at lower altitudes are arranged four other forms, alternately grey-, yellow-, grey- and yellow-bellied. Of the four lowland birds the two occupying western Abyssinia, which is damper than the east, are more richly pigmented than the others.

The actual records of the various forms are plotted in Map 4, which gives some indication of the complicated relief. Clearly the concept of sympatry and allopatry is not easy to apply. Lowland forms penetrate deeply into the highlands: along the Rift Valley a line of lowland grey-belly localities separates the eastern from the western highland grey-belly populations, while in the south-west the other lowland

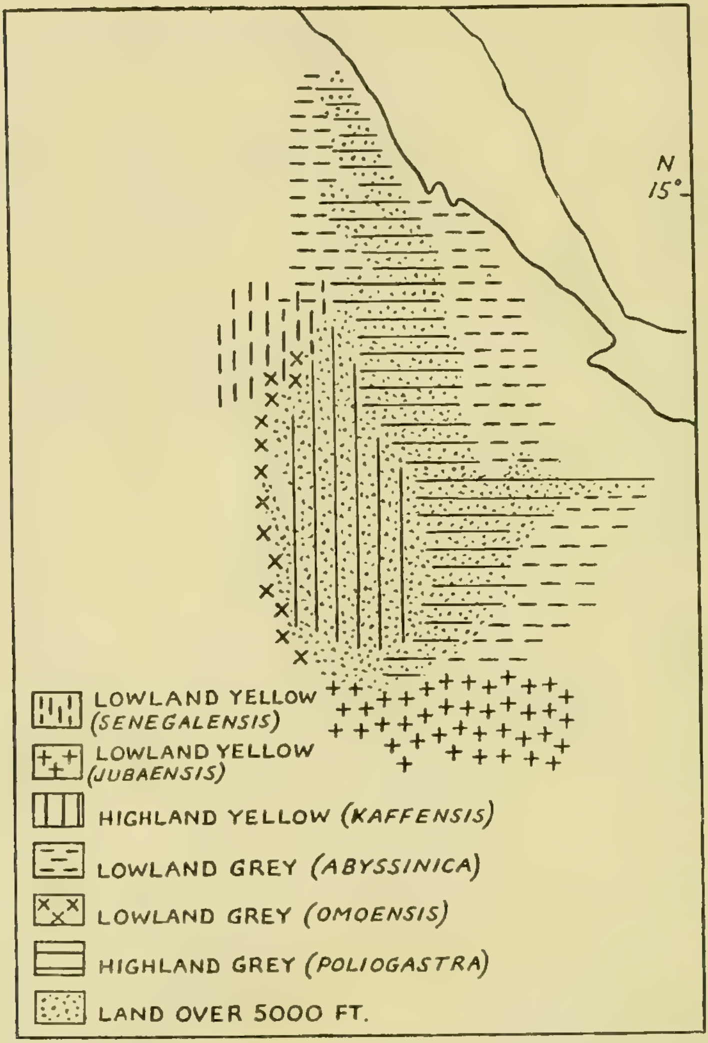
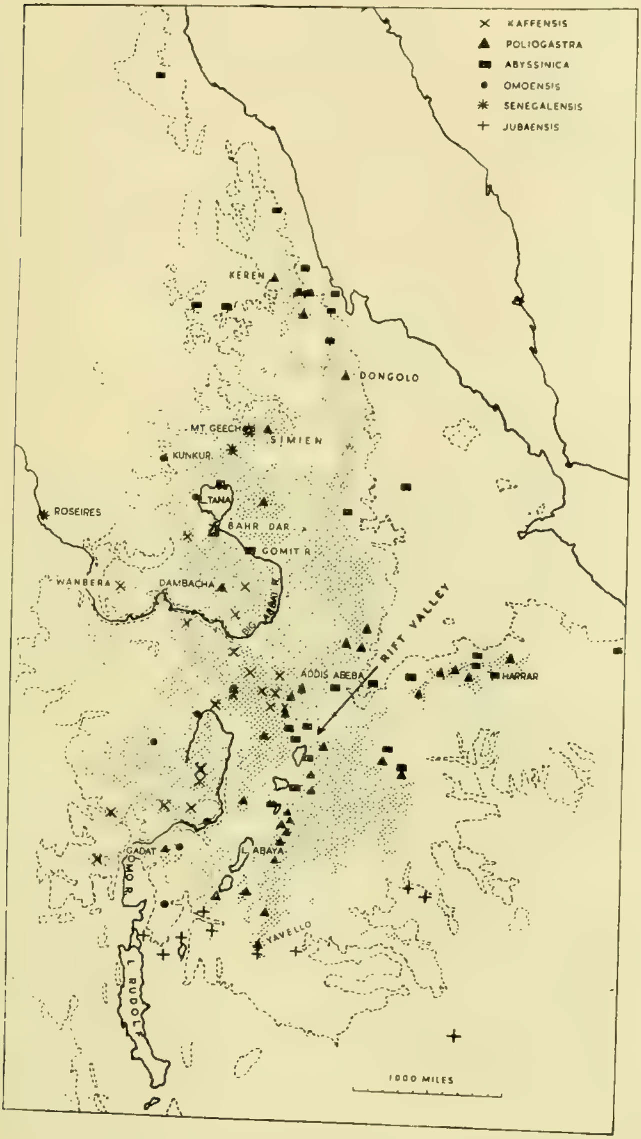

N
15°
LOWLAND YELLOW (SENEGALENSIS)
LOWLAND YELLOW (JUBAENSIS)
HIGHLAND YELLOW (KAFFENSIS)
LOWLAND GREY (ABYSSINICA)
LOWLAND GREY (OMOENSIS)
HIGHLAND GREY (POLIOGASTRA)
LAND OVER 5000 FT.

FIG. 9. Distribution (diagrammatic) of *Zosterops* belly-colour in N.E. Africa.


× KAFFENSIS
▲ POLIOGASTRA
■ ABYSSINICA
● OMOENSIS
✳ SENEGALENSIS
+ JUBAENSIS
KEREN
DONGOLO
MT. GEECH
SIMIEN
KUNKUR
ROSEIRES
TANA
BAHR DAR
GOMIT R.
WANBERA
DAMBACHA
BIG ABAI
RIFT VALLEY
ADDIS ABEBA
HARRAR
GADAT
OMO R.
ABAYA
YAVELLO
L. RUDOLF
1000 MILES

MAP 4. *Zosterops* distribution in N.E. Africa.

grey-belly (*omoensis*) occupies the Omo River valley, deeply cut through the country of the highland yellow-belly (*kaffensis*). Highland and lowland forms must in places actually meet. Two lowlands forms and also *poliogastra* have been recorded from Keren (Reichenow, 1903; Zedlitz, 1911), but this is an area of extremely broken country and it may be doubted whether the locality is critically stated. However, the specimens (in the British Museum) of both (grey-bellied) lowland *omoensis* and (yellow-bellied) highland *kaffensis* from Roke suggest overlap there; and there is a specimen of *abyssinica* from 9,000 ft. (= 2,750 m.), as noted on the label, at Bijo, near Harrar, right in the highland (*poliogastra*) zone. Again, Benson (1946*b*) at the extreme south of the range of *poliogastra*, near Alghe, recorded both this and the local lowland birds in juniper woods at 6,000 ft. (= 1,800 m.). One specimen from near Keren may be a hybrid between the highland *poliogastra* and the lowland *abyssinica* (see Note 4, Appendix 1). Finally, Mr. K. D. Smith (*in litt.*) encountered a mixed party of *abyssinica* and *poliogastra* at Faghena, on the eastern escarpment of Eritrea, on exotic trees in a clearing in the woodlands at 5,570 ft. This is an abnormally low altitude for *poliogastra* and the whole locality is peculiar ecologically.

The highland birds

In the highlands the grey-bellies (*poliogastra*) have a more extensive range than the yellow-bellies (*kaffensis*; see Note 5, Appendix 1). They occur all down the spine of the Eritrean and Abyssinian highlands, west over the plateau to near Lake Tana, east along the mountains towards Harrar and south to the end of the high country, at Yavello, east of the tip of Lake Rudolf. Grey-bellies everywhere occur on both sides of the line of the Abyssinian lakes, but they do not cross the deeply-cut valley of the Omo River just to the west. Beyond this the high-level *Zosterops* are yellow-bellies, which range from Lake Tana southwards.

The two forms apparently overlap a little. Both occur at Addis Ababa, with the yellows much the commoner (Guichard, 1950, and *in litt.*), and in the neighbouring Menengasha forest (B.M. specimens). The Addis overlap may be a recent recolonization following tree-planting of the formerly deforested area. Away to the north-west, south of Lake Tana, the Dembacha grey-belly (B.M. specimen; breeding condition), which is partly surrounded by yellow-belly localities, may indicate another limited area of overlap.

Both the grey-bellies and the yellow-bellies show some geographical variation. The former are a trifle smaller in the extreme southwest of their range (mean wing 61·5 mm. compared with 63·9). For an alleged plumage-difference between northern and southern grey-bellies, see Note 6, Appendix 1. Of the highland yellow-bellies (see Note 5, Appendix 1), those south of Nono are the most richly coloured, both above and below, and those from Shoa (the neighbourhood of Addis Ababa) which have been distinguished subspecifically, are the biggest, and a little duller generally, without such large and bright yellow foreheads. But, again, those from Nono and further north, within the bend of the Big Abbai (Blue Nile) are intermediate in these characters. Thus the variation is not a simple geographical cline and moreover plumage-colour is not correlated with rainfall.

I believe that the grey-bellies and the yellow-bellies of the highlands are conspecific. In the middle of their range both forms are the same size, with the same tail/wing ratio, and are similar in plumage (including eye-ring), except for the belly. Pending further field data, it seems that they form a parallel to the cases of the grey-bellies and green-bellies in the Cape (see section on " South Africa " below). True, in Abyssinia there is no evidence of interbreeding, but the ornithology of the country is such that it could hardly be expected at the present stage.

With their sharply defined yellow foreheads and comparatively long tails (ratio 75) the yellow-bellies of the western Abyssinian highlands differ from the nearest montane birds, on the Imatong group on the Sudan border, which have dimmer foreheads and shorter tails (70). The Abyssinian birds are more like some Kenya highlands birds, and though they differ from the nearest of these in having stronger carotenoid these appear taxonomically closer than the Imatong birds.

The lowland birds

As already mentioned, there are four main forms arranged round the highlands, grey-bellies and yellow-bellies alternately. In these birds also belly-colour has always been taken as a specific character but, as shown in Part 2, there is no reason to think this is correct and their true relationships are difficult to decide. All four forms are, as expected, smaller than the highland birds (see Appendix 3). The two eastern ones are particularly dingy in plumage, with reduced carotenoid and a tendency to muddy brownish wash on the underparts. These characters are not shared by the two western birds, the yellow-bellied *senegalensis*, which reaches Lake Tana from West Africa, and the lowland bird of south-west Abyssinia, with its clear grey belly (*omoensis*).

The difference in general colour tone between the eastern pair and the western pair of birds is connected with the fact that, apart from stronger carotenoid in the west, the melanin in these birds is of black (A) type, while in the eastern pair of birds it is of the browner (B) type. As discussed in Part 2, the taxonomic value of this character is uncertain. In so far as it depends on the humidity or aridity of the environment, as in South Africa, it is worthless. But in the West African *senegalensis* it has been shown that the melanin is of (A) type even in the driest environment. The occurrence of the same character in the contiguous *omoensis* might therefore mean taxonomic affinity ; but since *omoensis* inhabits the wettest environment of all the lowland birds, it might alternatively be, as hitherto believed, a form of *abyssinica*, climatically modified.

Geographical relations between lowland forms

The grey-bellies of the eastern lowlands extend from the Red Sea Hills (Erkowit) of the Sudan " wherever there is thick vegetation " (Cave and Macdonald, 1955) all down the eastern foot of the Eritrean–Abyssinian plateau ; and thence through the Rift Valley nearly to Lake Abaya and east through British Somaliland. They also occur down the western side of the Eritrean and Abyssinian highlands as far as Lake Tana and the beginning of the Blue Nile (Great Abbai) valley. Here they seem to overlap the yellow-bellies (*senegalensis*) from the west, which find their eastern limits on the western slopes of these Eritrean and Abyssinian highlands. Both forms have been collected near Keren and also on the shore of Lake Tana (see Note 7, Appendix 1), while the yellow-belly has also been taken on the slopes of Mt. Geech, where on geographical grounds the grey-bellied *poliogastra* (or even *abyssinica*) might have been expected, as will be seen from Map 4.

The other, south-western, grey-bellied form, *omoensis*, is typically represented from the northernmost point of the Omo River (Nono) southwards through the comparatively humid valleys in Jimma and Kaffa to the beginning of the flatter ground at the head of Lake Rudolf. Specimens from north of Nono are more puzzling, Gomit River birds (about fifty miles S.W. of Lake Tana—R. E. Cheesman, *in litt.*) are more like *abyssinica*, yet a bird from further north, on the west shore of the lake (Azobahr) is almost typical *omoensis*. Two more birds from Kunkur, still further to the north and west, are also more like *omoensis* than *abyssinica*, but they have dull upper parts—in other words, they are in this respect intermediate between the two forms, and these birds might be hybrids. But again, the dullness in plumage might be correlated with the fact that their environment is drier than normal for *omoensis* (see Note 8, Appendix 1). However, against both these hypotheses, Dr. Auber finds that the melanization of these dull-looking Kunkur birds is the typical (A) of *omoensis* without infusion of (B). In any case, although *omoensis* and *abyssinica* have not been recorded from the same locality anywhere, Map 4 suggests that round the west of Lake Tana they may overlap considerably; the big gap in the recorded distribution of grey-bellies just south of the Lake might be due to the accidents of collecting—much of the Blue Nile gorge is inaccessible.

On the whole, the ranges of grey-bellied *abyssinica* and *omoensis* and yellow-bellied *senegalensis* do not help to settle their taxonomic relationships. The extent of their geographical overlap and the absence of indubitable hybrids would in most groups of birds suggest specific separation, but in *Zosterops* the South African situation, described subsequently, shows that the ordinary rules do not necessarily apply.

On the east side of the mountains the widely-ranging lowland grey-bellies, *abyssinica*, are, so far as known, strictly allopatric with *omoensis*. This is not recorded east of the Omo Valley, while *abyssinica* is not known west of the Rift. A narrow ridge of highland, occupied by the montane *poliogastra*, intervenes between them. Also on the south of its range *omoensis* appears to be allopatric with the yellow-bellies (*jubaensis*; formerly *smithi*) occupying the arid country from the head of Lake Rudolf eastwards. Further, at least in Ethiopia these yellow-bellies seem allopatric with *abyssinica* on the north, though from lack of collecting it is not certain whether this relationship is maintained eastwards all the way through Somaliland (see Note 9, Appendix 1).

To summarize: in the east and south of Ethiopia *abyssinica*, *jubaensis* and *omoensis* are all allopatric; in the west *abyssinica*, *omoensis* and *senegalensis* all overlap round Lake Tana.

Geographical variations within the lowland forms

The local representatives of *senegalensis* (*sensu stricto*) are typical in colour, but the few specimens available from the Lake Tana–Mt. Geech area are abnormally large, as expected from the altitude. Their wings measure 59, 59 and 60 compared with 52–59 (but mean only 54·6) in the nearest (Sudan) birds at an average of 2,000 ft. lower.

The variation in the southern yellow-belly, *jubaensis* (see also *Bull. Brit. Orn. Club*, **72** : 50–51), is slight and in accord with expectation. Birds from higher altitudes, near Yavello, are a little bigger (wing 53·6) than they are further west, round Lake Rudolf (wing 52·1), or further east towards the Indian Ocean (wing 51·8), and perhaps not quite so dull-plumaged.

In the more widely ranging *abyssinica* the variations are more marked. In the first place, the most northerly birds on the African mainland, from Eritrea and the Red Sea Hills of the Sudan at an average altitude of 3,500 ft., are the smallest, wing 54·4 mm., compared with Abyssinian birds, *ca.* 4,500 ft., average 58·3 and British Somaliland, *ca.* 4,000 ft., average 57·1. All specimens from Abyssinia, Eritrea and the Sudan have brown beaks, a character unknown elsewhere in Africa except in *omoensis*. But all the British Somaliland birds have beaks more or less black. In plumage the northernmost birds tend to be more yellow-green above, not so dull (greyish) as the others.

Two populations of these grey-bellied birds are isolated by water, but both are little differentiated. Across the Red Sea birds of this type occur between about 1,500 and 5,000 ft. from near Mecca (that is, further north than the most northerly occurrence of *Zosterops* in Africa) to the Aden Protectorate, and they have been separated under the name *arabs*. In these birds the carotenoid is further reduced, so that they are even more dingy than Abyssinian *abyssinica*, with no yellow on the head and only slightly whitish lores. Moreover, they share the peculiarity of the brown beak. In dimensions they are extremely close to both Abyssinian and British Somaliland birds—wings 57·5 compared with 58·3 and 57·1 respectively, tail/wing ratio 73·5 compared with 72 and 73·4.

On the " continental " island of Sokotra, off Cape Guardafui, the tip of Somaliland, the birds average slightly brighter (more yellow-green) above than continental birds, though the yellow on the throat is no stronger, and they have little or no yellowish on the forehead. With wings averaging 56·1 and tail/wing ratio 71·8 they are not distinctive in dimensions. The beak is scarcely longer in proportion than in the mainland populations (beak/wing ratio 24·1 compared with 22·9–23·7), but it is interesting that it is not brown but black, like that of its nearest neighbours, in Somaliland. Thus the two isolated populations of *abyssinica*, though named, are " poor races ".

Provisional taxonomic conclusions

(1) The yellow-bellied and the grey-bellied highland birds, *kaffensis* and *poliogastra* are conspecific. It is not worth while to retain the name *schoana* as distinct from *kaffensis*.

(2) The grey-bellied lowland *abyssinica* is conspecific with the yellow-bellied *jubaensis* (*smithi*) and the grey-bellied *omoensis*.

(3) The yellow-bellied bird that enters western Abyssinia from West Africa (*senegalensis*) presumably belongs to a species different from (1), which looks so different, and from (2), which it overlaps.

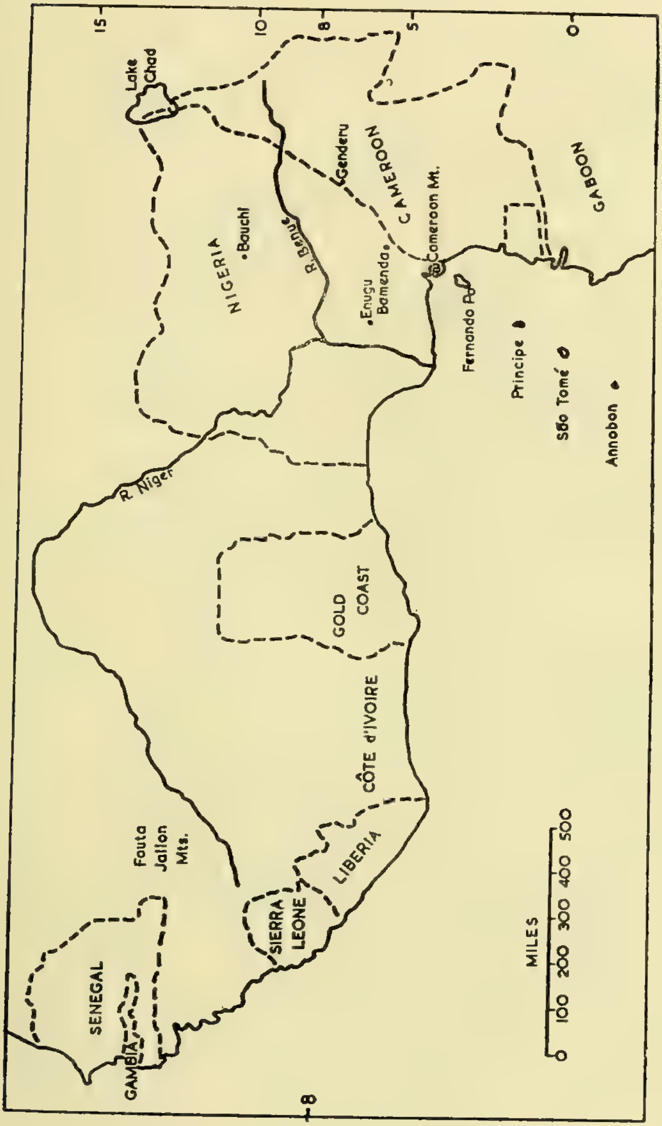
(4) The name *socotrana* is retained, on the character of the black, instead of brown, beak, but the range of the form is extended to include British Somaliland.

REMAINDER OF NORTHERN TROPICAL AFRICA

The whole northern savanna belt of Africa, south of about 14° N., is occupied by a brightly coloured *Zosterops* (*senegalensis*) with much yellow pigment and less melanin than any other form in Africa. It extends from the Atlantic (Senegal) almost to the coast of the Red Sea, from which its range is separated by the highlands of Eritrea and Abyssinia (Maps 1 and 4). Southwards the brightly coloured birds extend for an average depth of some five hundred miles towards the Equator with very little variation. Almost the whole of this vast area of nearly two million square miles is lowland, below 3,000 ft. The main exceptions are (*a*) the chain of small detached areas of plateau and mountain at the head of the Gulf of Guinea, (*b*) the Imatong group of mountains on the Sudan–Uganda border, (*c*) the western slopes of the Abyssinian highlands. (There are also the Futa Jalon massif in the west and the Bauchi plateau in eastern Nigeria, from neither of which is any *Zosterops* specimen available.)

The climate is driest in the north—predominantly thorn-bush country, merging southwards into " savanna " (tall grass with small deciduous trees) and ultimately, in the wettest parts, into tropical evergreen forest. The highlands carry some montane forest. In many parts of the area *Zosterops* seem to be uncommon and only about 200 specimens have been available for study.

From east to west through the belts of thorn country and savanna no local differences in plumage can be detected, though there are interesting differences in size (see Appendix 3, populations 13–18). Where, however, the rainfall is higher there are changes in plumage, chiefly connected with increases in melanin. Of the typically yellow *senegalensis* the most westerly representatives, from the Gold Coast to Senegal (Map 5), are the smallest—wing mean 53·5 mm. In Nigeria, the Cameroons and Oubangi-Chari the birds north of about 8° N. are larger, averaging 55·9, but in Southern Nigeria they are not (wings only 53·7). Further east, in the Sudan, birds north of 8° N. are about the same size (56·1) as those in the same latitudes in Nigeria and the Cameroons, but nearer the Equator, in the southern Sudan, extreme north-eastern Belgian Congo and the neighbouring corner of Uganda, they are smaller (54·6), much as in same latitudes in West Africa. As already noted in Part 3, these differences are closely correlated with the minimum temperatures. Then from slightly higher altitudes in the flat country of northern Uganda the few specimens available are a little larger than the foregoing, and finally the eight high-altitude specimens from 5,000–7,000 ft. on the western edge of the Abyssinian plateau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Fernando Po
Principe
São Tomé
Annobon
R. Niger
GOLD COAST
CÔTE d'IVOIRE
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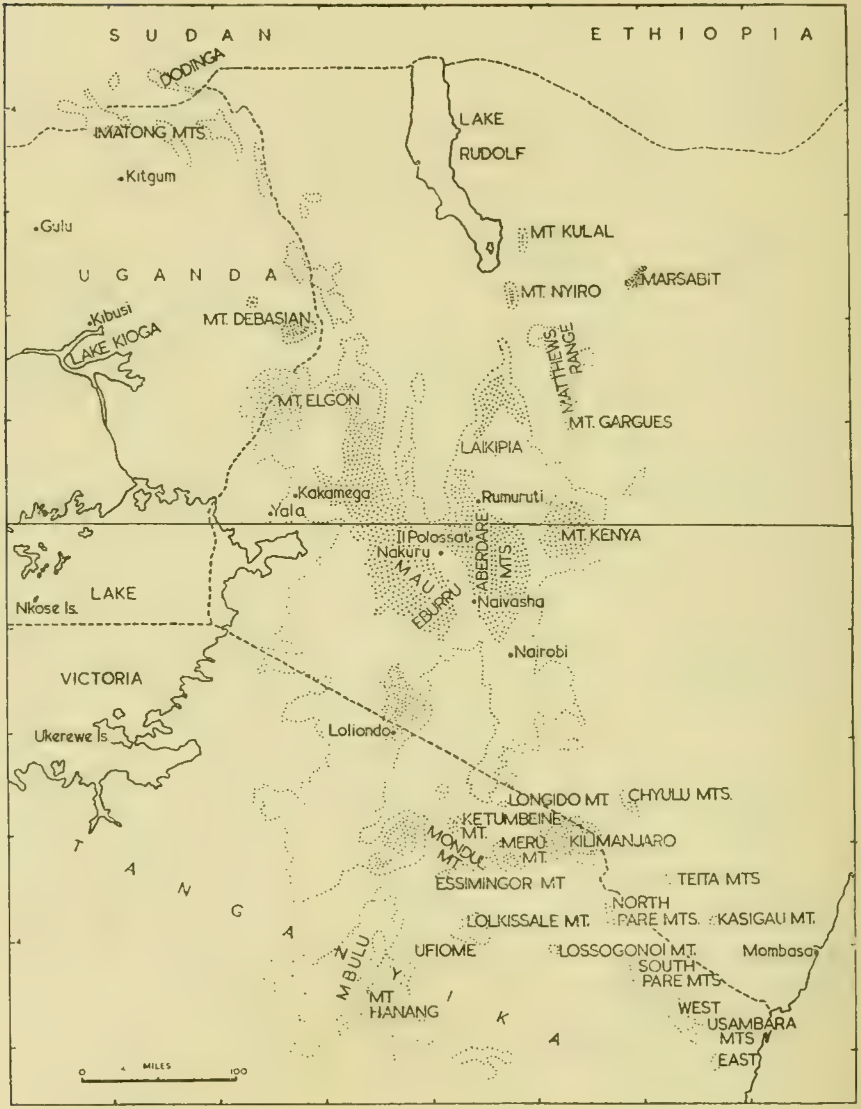
MAP 5. West Africa.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Kibusi
MT. DEBASIAN
LAKE KIOGA
MATTHEWS RANGE
MT. ELGON
MT. GARGUES
LAIKIPIA
Kakamega
Rumuruti
Yala
Il Polossat
MT. KENYA
Nakuru
MAU
ABERDARE MTS
EBURRU
LAKE
Nkose Is.
Naivasha
Nairobi
VICTORIA
Ukerewe Is.
Loliondo
LONGIDO MT
CHYULU MTS.
KETUMBEINE MT.
MONDUL MT
MERU MT.
KILIMANJARO
ESSIMINGOR MT
TEITA MTS
NORTH PARE MTS.
KASIGAU MT.
LOLKISSALE MT.
UFIOME
LOSSOGONOI MT.
Mombasa
SOUTH PARE MTS
TANGANYIKA
MBULU
MT HANANG
WEST USAMBARA MTS EAST
0 MILES 100

Contour at 4000 ft.

Map 6. Kenya and Northern Tanganyika.

and on the slopes of the Imatong group (Sudan–Uganda border; Map 6) are, as expected, the largest of all, with wings averaging 59·6 mm.

Apart from birds so much darker that they have received different names (dealt with below), the specimens can be divided into (*a*) the yellowest, (*b*) the greenest, (*c*) intermediates—the whole colour-range being small. The yellowest specimens are scattered through the whole range of *senegalensis*. The greenest birds, which, along with a few of the intermediates, can be matched with exceptionally bright specimens from the savanna belt south of the Equator (*anderssoni*), come from the high eastern localities just mentioned as providing the biggest birds.

Within West Africa the *Zosterops* change more markedly in plumage in the south-west corner, where the rainfall rises rapidly to over 120 inches. From the wet, forest, areas (rainfall over 80 inches, well-distributed) of Sierra Leone, Liberia and Côte d'Ivoire (Abidjan, rainfall 77 inches) all the specimens available are dark and dull, apparently owing to a general increase in melanin—i.e. as expected under Gloger's rule—without strengthening of carotenoid. (These birds have usually been called *leoninus* of Sclater, but as Rand (1951) has pointed out, this is a synonym of *demeryi* of Büttikofer.) These dark birds have wings even shorter (52·8 mm.) than the brighter birds to the north (53·5) and again the minimum temperature (68° F.) is exceptionally high. No detailed evidence is available of transition from the typically yellow *senegalensis* to the greener *demeryi*, though one specimen (" Kamasigi, Sierra Leone ") is intermediate. This lack of evidence is probably because collecting has been sporadic in this part of Africa and the belt of transition from dry country to wet is narrow.

East of the western Côte d'Ivoire, drier country comes right to the coast again until Nigeria is reached. Here dark birds can again be expected, but the present evidence from Nigeria is inconclusive (see Note 10, Appendix 1). Further to the south-east, however, round the Gulf of Guinea, the lowlands, which are exceptionally wet and hot, are occupied by the birds of the expected type (the so-called *pusilla*), small and richly coloured, with plenty of melanin giving them green upper parts and flanks, but also strong, slightly orange-tinged, carotenoid and a golden forehead. With wings 49–53 (mean 51·3), tails 30–33 (mean 31·5), these birds are the smallest in Africa—in accord with the high local minimum temperature, 69° F —and they also have the lowest tail/wing ratio (61) except for the similar neighbouring birds from Manenguba (see below). Birds of this type occupy the southern Cameroons and Gaboon south to at least 1° 45′ S. (Mbigou) and east to at least 16° E. Most of this area receives between 70 and 120 inches of rain, well distributed, and evergreen forest abounds. It is, in fact, on the north-western edge of the great Congo forest; and similar birds probably exist in a narrow belt along the edge of the forest right across the north of the Congo Basin. However, the only skins from this belt, which come from Medje, a thousand miles to the east, though recorded as *pusilla* (Chapin, 1954), differ somewhat—see below—so that if specimens become available from intervening localities they may be expected to show an east–west cline.

At their western end these little " *pusilla* " abut upon the mountainous area along and close to the Nigeria–Cameroons border, with Cameroon Mt. (13,000 ft.) on the shore of the Gulf of Guinea and 100 miles to the north-east the Bamenda–Banso highlands (7,000 ft.), which tail off northwards past Genderu into the flats round Lake Chad. Between Cameroon Mt. and Bamenda smaller isolated highlands occur—Manenguba, Kupe, and the Rumpis. Serle (1950, 1954) has shown that all these highlands are occupied by richly coloured *Zosterops* (with plumage like that of the lowland " *pusilla* "), which have all been called *stenocricota*, a form described from Cameroon Mt. Also in these mountains several *Zosterops* have been collected that are so dull and dark that they have been regarded as a different species (*Z. phyllica*). They appear, however, to be merely cases of individual deficiency in carotenoid (Moreau, 1953).

The specimens from the highest average altitude, 6,000 ft. in the Bamenda–Banso highlands, are the biggest—wing-mean 58·7 mm., tail/wing ratio 65·5. From an average of 4,000 ft. on the Kupe, Manenguba and Rumpi Mts. the birds are much smaller, wing-mean 53·1, tail/wing ratio 58. The birds of Cameroon Mt., which occupy it up to over 9,000 ft., may well be larger at the higher levels, but those specimens labelled with an altitude come from an average height of only 4,000 ft. and average small—wing-mean 54·2 mm., tail/wing ratio 62. Each of these populations has a tail disproportionately short when compared with birds of similar wing-length anywhere else in Africa, as already discussed in Part 3. The biological significance of this peculiarity, localized round the head of the Gulf of Guinea, is unknown.

While the strong melanin of these Cameroon birds, both montane and lowland, is regarded as correlated with the high rainfall, the general appearance of their plumage differs from that of the other dark, high-rainfall, *Zosterops* of West Africa, those of Sierra Leone and Liberia, in being brighter, evidently as a result of stronger carotenoid throughout. The highland birds are indeed so like some on mountains in East Africa that some workers, though not Bates (1930) nor Serle (1950), have regarded them as conspecific and not closely allied to the surrounding *senegalensis*. This conclusion would fit with the remarkable affinity between the montane avifauna of Cameroon Mt. as a whole with that of East Africa. Half the passerines of Cameroon Mt. belong unquestionably to East African species and, though no geographically intervening specimens are known, some of the birds are not even subspecifically distinguishable —see Moreau (1952) for discussion.

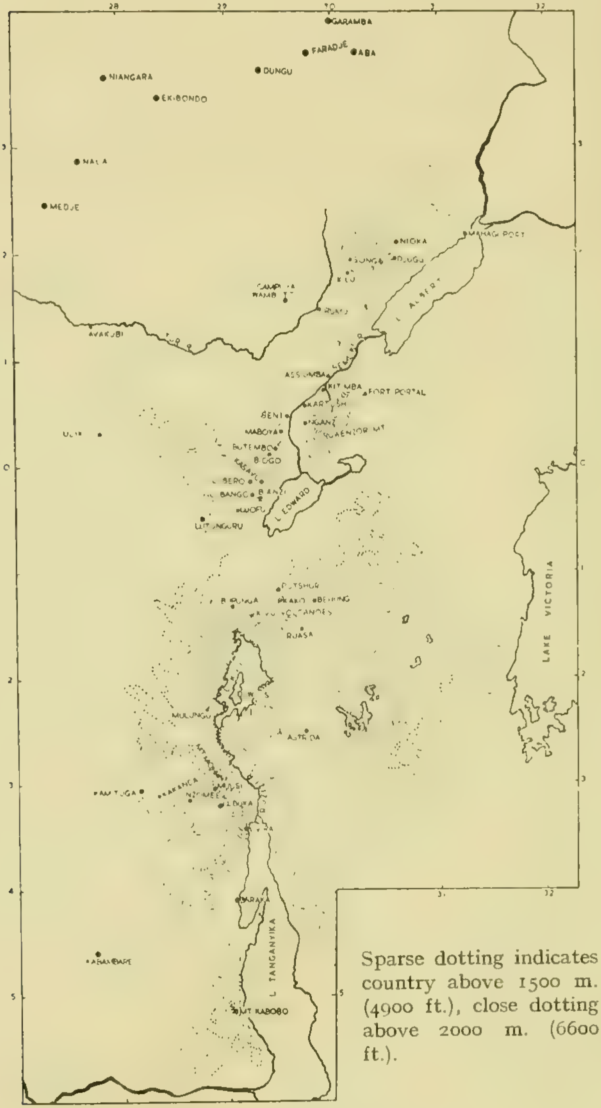
The idea of specially close affinity between *stenocricota* and montane birds elsewhere must, however, be rejected. In the first place, the *Zosterops* (*stenocricota*) of the mountains differ only in size—and that, no doubt, clinally—from the *Zosterops* ("*pusilla*") of the lowland forest at their feet. Actual transition to typical yellow *senegalensis* is shown so far only by three specimens which are intermediate in both colour and tail/wing ratio between *stenocricota* and *senegalensis* ("*genderuensis*" Reichenow), from 100 miles north of the Bamenda highlands, where the country is somewhat lower and drier. Collecting in the lowlands east and west of Bamenda may be expected to yield further intermediate specimens; but owing to the closeness of the isohyets the belt of transition is probably narrow. To the west no specimens are at present known from nearer than Enugu (100 miles away), a savanna locality where the birds are typically yellow *senegalensis*, and to the east the situation is rather similar (see Note 11, Appendix 1).

Cameroon Mt. differs from every other in the African continent in possessing two Zosteropids of undoubtedly different species, for its higher parts are inhabited by both *stenocricota* and the highly aberrant *melanocephala*, which appear fully sympatric and which associate together on the trees (Serle, 1950). With its black and brown plumage, pale beak and general loss of carotenoid, *melanocephala* differs so greatly from all others on the African continent that it has usually been kept in a separate genus, *Speirops*, along with other aberrant birds on the islands in the neighbouring Gulf of Guinea. There also each *Speirops* occurs alongside a more normal *Zosterops*. These are discussed in Part 5 below, and because the situation on Cameroon is so like that on the islands discussion of *melanocephala* will be postponed.

Further east, through the southern zone of the savanna and as far as the north-eastern Belgian Congo and Uganda, typical "yellow" *senegalensis* persist without change of plumage to south of 3° N. There incipient change can be detected. In the Congo (Map 7), while birds from Niangara (3° 35′ N., 27° 50′ E.; in savanna) appear typical, those of Garamba (4° 10′ N., 30° E.) and also Ekibondo (3° 32′ N., 28° 24′ E.) are a trifle greener, while at Medje (2° 26′ N., 27° 17′ E.) in a wetter, forest, climate, the birds are much darker. As already noted, they have gone by the same name (*pusilla*) as the equally small birds a thousand miles to the west, but at Medje they are not quite so short-tailed (ratio 65 against 62) and are much less yellow on the forehead. *Zosterops* do not seem to extend further south towards the centre of the Congo Basin (cf. the blank shown on Map 1). Chapin (1954) living for a year at Avakubi, eighty miles nearer to the equator, never recorded a *Zosterops*.

As already noted, in the extreme east of the range of *senegalensis*, on the borders of the Sudan, the birds become greener as they ascend the mountains on the Sudan border (the Imatongs, Didingas and Dongatona). The *Zosterops* associated with the forests on the tops of these mountains have nearly as much melanin as those on the mountains of the Cameroons, though not quite such rich yellow, and are indistinguishable from birds on the mountains round Lake Nyasa, over a thousand miles to the south and on the other side of the equator. This occurrence of "yellow" and "green" *Zosterops* on the same small mountain will be further considered when the more numerous examples in the Nyasa area come to be dealt with. Meanwhile, it seems that the green Imatong birds, like those of the Cameroons highlands, are derived from the surrounding "yellow" *senegalensis* and owe their resemblance to each other and to the Nyasa birds to convergent evolution in similar climates.

South of the Imatongs, in Uganda north of about 1° N. (which is dry), the *Zosterops* are a trifle greener than typical *senegalensis*. It seems certain that this indicates transition to the distinctly greener birds, long known as *stuhlmanni*, in the country with higher and better-distributed rainfall on the northern and western shores of Lake Victoria (Maps 6 and 7). These birds differ in plumage from those of the tops of the Imatongs (and elsewhere) only in a slightly warm tinge, which has been described as "cinnamon". More collecting is needed to establish this transition


28
29
30
32
GARAMBA
FARADJE
ABA
DUNGU
NIANGARA
EKIBONDO
NALA
MEDJE
NIOKA
MAHAGI PORT
SUNGA
DJUGU
KILO
AVAKUBI
L. ALBERT
ASSUMBA
FORT PORTAL
BENI
MABOYA
BUTEMBO
BOGO
L. EDWARD
LUTUNGURU
RUASA
LAKE VICTORIA
MULUNGU
L. TANGANYIKA
MT KABOBO
0
1
2
3
4
5

Sparse dotting indicates country above 1500 m. (4900 ft.), close dotting above 2000 m. (6600 ft.).

Map 7. Central Africa.

in Uganda thoroughly (see Note 12, Appendix 1) and some discontinuity may be expected from the long east-and-west barrier interposed by the swamp belt of Lake Kioga and associated waterways. This transition is important in interpreting the taxonomy of the African *Zosterops*, because, as will be shown below, the Lake Victoria birds lead gradually to populations with plumages as richly green as any in Africa.

Summary

Bright yellow *Zosterops* extend from Senegal to the western slope of the Abyssinian plateau. In size they vary consistently with climate and altitude, always averaging larger in higher and/or cooler localities. Wherever the rainfall in the lowlands is such as to give a "forest climate", the birds show more melanin ; but the resultant plumages are slightly different in the four detached wet areas, Sierra Leone—Liberia, head of the Gulf of Guinea, north-eastern Belgian Congo, and southern Uganda. Transition from "yellow" to "green" birds appears to take place in all these cases in a few miles distance, in conformity with rapid change in climate. The two mountain groups that are surrounded by "yellow" *senegalensis*, at the head of the Gulf of Guinea and on the Sudan–Uganda border, are both occupied by larger and greener birds. Here again, transition from the lowland, yellower, type is believed to take place.

It is concluded that (except the aberrant bird of the top of Cameroon Mt.) the whole of the birds considered in this section belong to the same species, *senegalensis* ; the subspecific names that can usefully be applied are *demeryi* for the greener birds of Sierra Leone, *stenocricota* for the greener birds round the head of the Gulf of Guinea and eastwards and *stuhlmanni* for the greener birds on Lake Victoria.

KENYA AND NORTHERN TANGANYIKA TERRITORY

This area (Map 6) differs from all others considered in the number and abrupt isolation of its ecological (montane) islands and, conformably, in the number of its well-marked forms of *Zosterops* (Text-fig. 10) within a small area. The lowland birds have always been regarded as specifically distinct from the highland, which is doubtless correct, and there has been great diversity of opinion about the specific allocation of the highland birds. Essentially, the area consists of dry thorn-bush and "savanna", nearly all with rainfall under 30 inches, out of which rise the Kenya Highlands and an archipelago of smaller highlands, each bearing some montane forest, but effectively isolated from each other by lower, hotter and drier country.

The Kenya Highlands extend about 150 miles each way, at altitudes of at least 5,000 ft., with several parts rising to 10,000 ft. and over. Much montane forest, which has certainly been more continuous in recent historical times, still exists throughout the Kenya Highlands, but they are deeply penetrated by savanna. In particular the Rift Valley past Nakuru and Naivasha is far drier than the mountains on either side ; and although it is narrow and much of its floor is over 5,000 ft. a.s.l., it is something of a barrier for forest organisms.

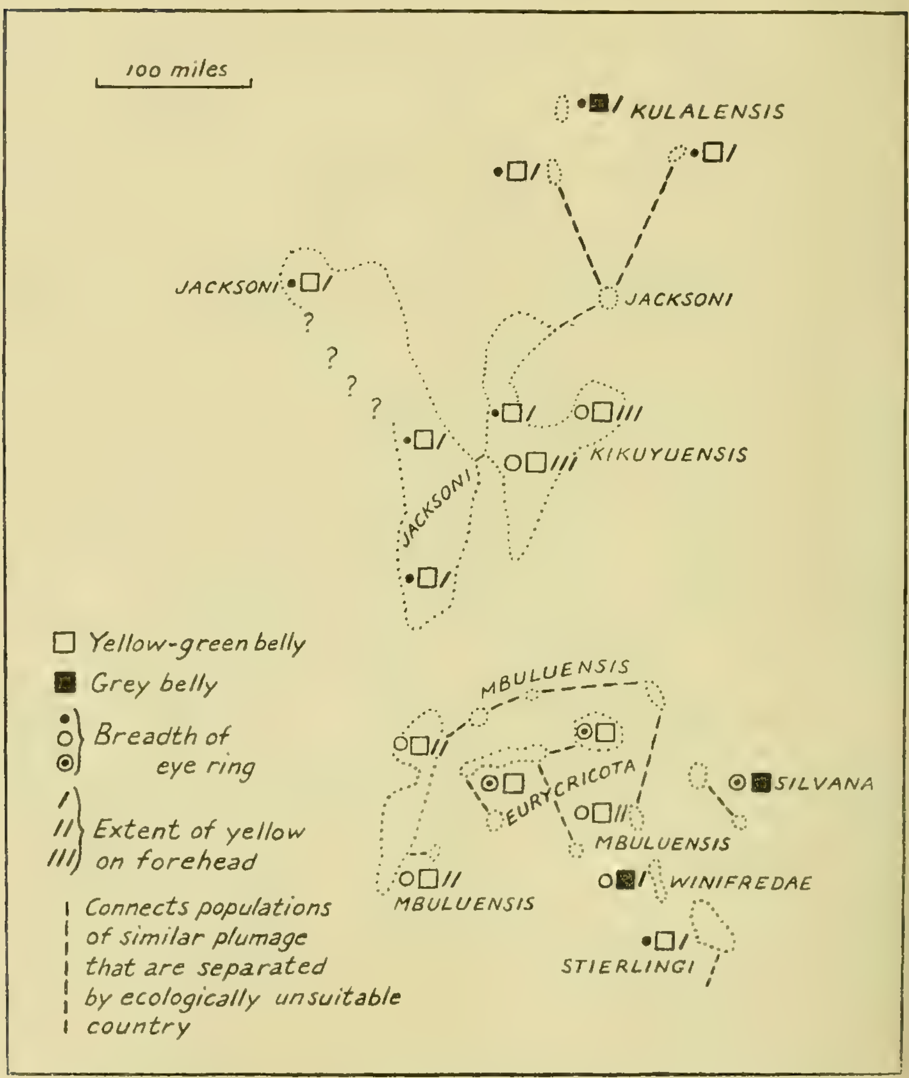

100 miles
KULALENSIS
JACKSONI
JACKSONI
JACKSONI
KIKUYUENSIS
Yellow-green belly
Grey belly
Breadth of eye ring
Extent of yellow on forehead
Connects populations of similar plumage that are separated by ecologically unsuitable country
MBULUENSIS
EURYCRICOTA
SILVANA
MBULUENSIS
WINIFREDAE
MBULUENSIS
STIERLINGI

FIG. 10. Geographical distribution of characters in East African *Zosterops*.

The less extensive highlands of East Africa range in size from Kilimanjaro, which rises to nearly 20,000 ft. and carries a great girdle of forest, to Kasigau and Marsabit, each a little over 5,000 ft. with a forest cap, and the anomalous East Usambara plateau, with a forest covering that, thanks to proximity to the Indian Ocean, extends practically down to sea-level.

The dry country separating the various highlands is occupied by a small, rather pale, yellow-bellied *Zosterops* that surrounds all the montane forms. This type of bird is palest and greyest in the north-east, where, on the Abyssinian border, we have already met with it, from Lake Rudolf to the Indian Ocean, under the name *jubaensis*. Further south, down the coast[1] and also inland, birds of this type become slightly greener above (less grey) as the altitude and rainfall increase. Finally, in the neighbourhood of Nairobi and again in Mbulu,where they reach as high as 6,000 ft. a.s.l., these non-forest *Zosterops* (here usually called *flavilateralis*) are birds of yellow-green upper parts and lemon-yellow underparts with some green on the flanks. Even at their brightest and freshest they have, however, a certain "dusty" look, shared by no other yellow-bellied *Zosterops* on the continent. As noted previously, this effect is probably due to the nature of their melanization (B type).

These dry-country birds increase in size with increasing altitude, as expected. The specimens from below 4,000 ft. (average altitude 2,500 ft.) have mean wing-length 54·0 mm., those from higher altitudes (averaging 5,000 ft.), 55·3 mm. It may be added that in this dry habitat the *Zosterops* probably move about a good deal, with corresponding increase in gene-flow.

These savanna *Zosterops* and the montane birds that they surround can hardly be regarded as geographically separated, for on the slopes of the mountains savanna and secondary bush interdigitate with the forest, which, owing to human interference, is nearly everywhere in retreat. Moreover the ecological separation between montane forest and savanna *Zosterops* is not complete, since both are liable to frequent secondary growth and introduced trees. Mr. A. Forbes-Watson *in litt.* has noted that in the Teita Hills at over 5,000 ft. both the local mountain birds (*silvana*) and the savanna birds frequent the same (non-primary) vegetation and that the same species of fruit can be found in the stomachs of both. Actual mixed feeding-parties of highland and lowland *Zosterops* have been noted in a garden near Nairobi (*kikuyuensis* and *flavilateralis*, Mr. J. G. Williams *in litt.*) and in exotic trees in Mbulu (*mbuluensis* and *flavilateralis* in *Grevillea* used as coffee-shade, Dr. G. Zink *in litt.*).

There is no suggestion of hybridization between the two forms and no difficulty in distinguishing the montane birds from those of the surrounding savanna anywhere in Kenya or Northern Tanganyika except in Usambara. There montane and savanna birds begin to converge in appearance, with a consequent problem of differentiation that continues southwards through Tanganyika Territory.

So far as known, all the East African mountains that retain any forest are inhabited by montane *Zosterops* (see Note 14, Appendix 1), even such small and isolated mountains as Marsabit and Kasigau. Their differentiation is remarkable for, apart from smaller variations, there are eight forms so unlike in appearance that they have been allocated among five different species. Five of the eight forms occur east of Kilimanjaro, within a space of 250 miles; and of these five each is within sight of the stations of at least two others. Two of the geographical gaps do not exceed twenty miles. Thus, although the differences between the forms are not so great, the *Zosterops* situation in this ecological archipelago of East Africa is comparable to that of the *rendovae* group, isolated from each other by sea, in the Solomon islands, to which Mayr (1947) has drawn attention.

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[1] It appears to be a fact, and one for which no explanation can be offered, that in southern Kenya and all through Tanganyika Territory, *Zosterops* are extremely rare in the comparatively damp coastal strip, the vegetation of which appears to be thoroughly suitable for them (see Note 13, Appendix 1).

In the East African montane birds the main variation is in three characters, the distribution of which is shown diagrammatically in Text-fig. 10:

> (*a*) The birds of Kulal in the north, Teita and South Pare (N.E. and S.E. respectively of Kilimanjaro) have grey bellies. All the rest have bellies more or less green and yellow.
>
> (*b*) Eye-rings are biggest in Kilimanjaro and Teita birds, up to 5 mm. broad and covering much of the side of the head; smaller but still bigger than elsewhere in Africa (up to 3 mm. broad) in the eastern Kenya highlands and in an arc round the north of Kilimanjaro, Mbulu–Chyulu–North Pare; smallest in the north, northwest and southeast.
>
> (*c*) Golden foreheads are particularly large and rich in the eastern Kenya highlands; somewhat less marked in Mbulu-Chyulu-North Pare; entirely absent on Kilimanjaro and Teita; and intermediate elsewhere.

In Kenya west of the Rift the highlands (above about 6,000 ft.), from Mt. Elgon to Loliondo, are occupied by a large, rather dull-coloured green bird (*jacksoni*) with rather small eye-ring and a yellow forehead that is usually narrow but sharply defined. The carotenoid throughout the plumage is rather "colder", less golden, than that of the other montane *Zosterops* of East Africa. The most northerly birds, those on Elgon, tend to have less sharply-defined foreheads (so that some females look like South African and Nyasaland birds) and to be slightly yellower than those of the main West Kenya Highlands. (But I agree with those who hold that they do not merit the separate name *elgonensis*.) These tendencies, if slightly exaggerated, would produce a bird like those inhabiting the tops of the Imatong group of mountains on the Sudan border (top left-hand corner of Map 6), about 200 miles to the north of Mr. Elgon. This Imatong type is believed to have arisen there by local evolution (see preceding section) and the resemblance is to be borne in mind when considering the classification of the African *Zosterops* as a whole.

Within the western Kenya highlands the size of the birds varies, at least in part as expected from the altitudes. The largest birds (wing 62·0 mm.) are in the centre, between Elgon and Naivasha and including the Mau, at a mean altitude of 8,500 ft. Further south, mean altitude 7,000 ft., wings average only 60·6 mm. Also in the north, from Mt. Elgon itself, the birds are small (wing 60·6), but the few specimens available with altitude data average only 7,000 ft.

It is not certain what relationship the *jacksoni* of the western Kenya Highlands bear to the much yellower *stuhlmanni* of the shores of Lake Victoria, a bird regarded in the preceding section as transitional from the yellow *senegalensis* of West Africa. From Mr. Elgon westwards for at least 100 miles no *Zosterops* seems to be known in collections. However, south of Elgon, from an area less than 100 miles square, mostly at about 4,500–5,000 ft., round Kakamega and the basin of the Yala River, the birds (described by Van Someren as *yalensis*) are brighter than *jacksoni*, with less melanin generally, and are smaller (wing 58·3 compared with 62·0). In their slightly yellower plumage and, in some individuals, less defined yellow on the forehead, the Yala birds show a tendency towards the Lake Victoria birds. No cline is, however, demonstrable because nearly 150 miles intervene between the Yala localities (see Note 15, Appendix 1) and the nearest *stuhlmanni* specimens.

Birds of *jacksoni* type extend east across the Rift Valley in a puzzling fashion, which does not seem to have been realized hitherto. This will be reverted to later. Meanwhile the point to make is that most of the Kenya Highlands east of the Rift are occupied by a strikingly different bird, *kikuyuensis*, one of the most showy *Zosterops* in Africa, with very large golden patch on the forehead and a broad white eye-ring. Apart from the usual larger size at higher levels, the Mt. Kenya birds are indistinguishable from those further south, to beyond Nairobi, and from the Aberdares (see Note 16, Appendix 1). It is unfortunate that the various specimens in collections labelled "Aberdares" bear no precise localities or altitudes, because somewhere towards the north end of the range there seems to be contact with birds of *jacksoni* type, and it is important to know what their relations are.

Typical *jacksoni* come right to the wooded western edge of the Rift Valley, including the Eburru spur, which projects just north of Lake Naivasha to within ten miles of the east side of the Rift (there formed by the western foot of the Aberdares). From this side of the Rift various collections possess birds of *jacksoni* type labelled Naivasha, Il Polossat (at 7,000 ft. about fifty miles north of Naivasha), Rumuruti and Laikipia. These localities are all on the northern end of the massif of which the Aberdares form the crest and the local *jacksoni* appear to be separated by no ecological barrier from the Aberdares *kikuyuensis*. In particular, the forest at Il Polossat is "mixed, with juniper, just the same as on the Aberdares" (J. G. Williams *in litt.*). Are then these birds allopatric? In any case the distances involved are very small and there is no sign of intergradation or hybridization between these two very different forms of *Zosterops*, both of which are essentially highland.

The eastern birds of *jacksoni* type themselves form part of an interesting series. All the seven specimens from the area Naivasha–Rumuruti are a trifle yellower than typical *jacksoni*, but they are equally large. Sixty miles to the north-east, across a belt of dry thorn-bush, rather similar birds reappear on Gargues Mt. (about 8,800 ft.), the southern end of the Matthews Range, but they are smaller (four average 59·6 against 62·0) and also duller, with a trifle less of both melanin and carotenoid. These birds may or may not extend along the whole seventy miles of the Matthews Range ; but on Mt. Nyiro (about 9,000 ft.), just detached from the northern end, the birds are slightly different. They are of the same "difficult", generalized, type but rather larger than the Gargues birds and very variable in plumage. The seven Nyiro birds available average 62·5 mm. in wing compared with 59·6 in the Gargues. In plumage the Nyiro birds range from almost typical *jacksoni* to markedly duller and paler, like those of Gargues. (It is difficult to understand why Jackson and Sclater (1938) attributed Nyiro and Orr Valley specimens to the Abyssinian subspecies *kaffensis*, which has the carotenoid more golden and the forehead brighter and more defined.)

To the east across eighty miles of thorn-bush, the *jacksoni* type of bird reappears, still further "attenuated", on the small volcano Marsabit, which rises to only 5,500 ft. The forest is of a very dry type, with much *Juniperus*, and the rainfall exceptionally low for any sort of evergreen forest—only 32 inches at the meteorological station 1,000 ft. below the summit. Twelve Marsabit birds are all dull-coloured and markedly small (wing 57·5)—but still quite different from the *jubaensis* (yet smaller and of a "dusty" pallor) of the surrounding thorn-bush. Thus we have a west-to-east cline of decreasing pigment and size on the three highlands, Laikipia–Gargues (Matthews Range)–Marsabit, all strongly isolated.

As noted, the birds of Mt. Nyiro, off the north end of the Matthews Range, do not conform with the Laikipia–Marsabit trend: they are larger and not so dull-coloured. Their tendency in these respects is towards the *Zosterops* (*kulalensis*—see Note 17, Appendix 1) of the forest belt on Mt. Kulal (7,700 ft.), an old volcano forty miles to the north and also isolated by very dry country. The available specimens (from 6,000–6,500 ft.) have the same wing-average, 62·5, as the Nyiro birds, but they are grey-bellied and perhaps also have rather longer tails and beaks. In other respects they resemble the Nyiro birds more closely than any others (and particularly than any of the Abyssinian birds, the nearest montane neighbours to the north). This situation finds an almost exact parallel in the relationship (described below) between the grey-bellied *winifredae* of the South Pare mountains and the yellow-bellied birds of the Usambaras a few miles to the south. And in fact morphologically the Kulal birds are to the South Pare birds just as the Nyiro are to the Usambara. The first two mentioned, which there is no reason to regard as closely related, show the same degree of convergence as the second pair.

Reverting to the main eastern Kenya islands, for about 150 miles south from the southern end of *kikuyuensis*, near Nairobi, no montane *Zosterops* is known. Then, in the neighbourhood of Kilimanjaro and the Tanganyika border there are a number of forms. Birds resembling *kikuyuensis* in their broad eye-rings, but with less marked golden foreheads and less green on the underparts, appear in an arc of small mountains surrounding Kilimanjaro on the north, from the Mbulu Highlands and Mt. Hanang on the west, through Ketumbeine, Longido and the Chyulus to the North Pare Mts. (*mbuluensis*)—see Note 18, Appendix 1. A typical *mbuluensis* is known also from Essimingor Mt., of which more later. The very variable birds from the two extreme stations, Mbulu and North Pare, cannot, in series, be distinguished in plumage. (The fact that the latter average a little smaller, wing 60·4 compared with 62·5, is presumably at least in part because they come from altitudes averaging 1,000 ft. lower.) Yet between them intervenes Kilimanjaro, with a very distinctive *Zosterops*—*eurycricota*, with the largest size of eye-ring (up to 5 mm. broad), completely green forehead in nearly all specimens and, as a rule, much deep green and no bright yellow on the underparts. The difference between typical *eurycricota* and typical *mbuluensis* is striking, but individual variation is such that slight overlap occurs in each of the characters mentioned.

Z. eurycricota extends westwards from Kilimanjaro, wherever there is forest, along the highland that connects Mt. Meru and Mondul Mt. with Essimingor, which is separated from Mbulu only by the twenty-five miles of the Rift Valley. Two specimens from Essimingor are exactly like Kilimanjaro birds, yet the third specimen known from this small mountain is the equally typical *mbuluensis* already mentioned. It is difficult to know how to interpret this. It could mean that *eurycricota* and *mbuluensis* belong to different species ; but perhaps the *mbuluensis* is a straggler from across the Rift Valley. A good sample of the Essimingor population is needed, especially as a basis of comparison for the future, in case one type of *Zosterops* is here replacing another.

Birds like those of Kilimanjaro reappear in the attenuated forest on Lolkissale Mt. and the edge of the Lossogonoi plateau, fifty miles south of Kilimanjaro and cut off by arid thorn-bush. The only difference is that most of the Lossogonoi and Lolkissale specimens have a slight golden wash on the forehead, a feature that is very rare in the Kilimanjaro–Meru–Mondul population.

About fifty miles east of Kilimanjaro, across, as it were, the Mbulu–Chyulu–North Pare arc, the grey-bellied birds of the Teita Hills (*silvana*) resemble the Kilimanjaro birds in their very large eye-rings and otherwise entirely green heads. Also they share with them the highest tail/wing ratio in East Africa, over 78. They differ in having a higher beak/wing ratio and more melanin generally—enough to make their throat greenish rather than yellowish—and a bright yellow edge to the "bend of the wing". This contrasts so sharply with the green of the rest of the upper parts that it is conspicuous in the field (M. E. W. North, *in litt.*) and at first strikes one as a peculiar feature. It is, however, only an exaggeration of the tendency, visible in a few *eurycricota*, for the tiny feathers on the bend of the wing to be slightly yellower than their neighbours. On the whole the Teita birds are undoubtedly more closely related to the Kilimanjaro than to any others.

The Teita form is of special interest because it exists in exceptionally small numbers for a continental *Zosterops*. Fortunately for its survival, it is not entirely dependent on the few hundred acres of primary evergreen forest that remain in the patches. It has been observed in secondary *Albizzia–Gummifera–Combretum* woodland in the mountains, in flocks alongside, but not mingling with, flocks of the yellow savanna bird, *flavilateralis* (A. Forbes Watson, *in litt.*), and stomachs of both birds contained the same food. M. E. W. North estimates that the total population of *silvana* throughout the Teitas may be under 2,000 ; but similar birds inhabit the little cap of forest on Kasigau Mt., over fifty miles to the east and separated by arid thorn-bush.

These grey-bellied Teita birds are only fifty miles from the Pare Mts. On the north end of this chain the yellow-bellied *mbuluensis* occurs, as already mentioned. Further south, the middle of the chain is lower and probably too dry for montane *Zosterops*, but towards the southern end, after an interval of some forty miles, montane forest reappears and is there inhabited by the last of the three grey-bellied birds of East Africa, *winifredae*. Apart from the belly-colour, these birds are rather intermediate between their northern neighbours, in North Pare, and their southern neighbours in the mountain forests of Usambara less than twenty miles away across the semi-desert Mkomasi gap. This might be due to clinal environmental influences of some sort, or, in view of the small distances, to gene-flow from both directions. The South Pare birds have carotenoid less golden than the North Pare, less prominent yellow on the forehead and tail/wing ratio lower—73 compared with 75. All these differences are tendencies towards the Usambara birds, which have slightly smaller eye-rings, less rich coloration and tail/wing ratio only 69. This Usambara type of bird extends down through Tanganyika Territory nearly to the Zambesi, and is further discussed in the section "Southern Tropical Africa". It is remarkable that on the East Usambara Mts., where evergreen forest extends down the seaward slope nearly to sea-level, the montane *Zosterops* in question stops at the edge of the plateau, at about 3,000 ft. Incidentally, no "savanna" *Zosterops* has been found round this seaward foot of the mountains or on the neighbouring coastal plain.

Summary and classification

Zosterops show sharper differentiation in this area than in any other. But among the montane forms extent of differentiation is not related to the extent of existing ecological barriers.

The three grey-bellied forms each appear to be more closely allied to their nearest yellow-bellied neighbours than to any other *Zosterops* and not to be specifically distinct from them.

On the same highland, at the north end of the Aberdares, *jacksoni* (from the west) and *kikuyuensis* (from the south) appear to meet allopatrically, without ecological barriers and without hybridization. This could mean that they belong to different species. The same applies to the occurrence of both *mbuluensis* and *eurycricota* on Essimingor but, partly because these forms show some overlap in characters, a different view is preferred.

Apart from the belly-colour of the South Pare birds, the four montane populations of Usambara, South Pare, North Pare and Kilimanjaro, at first sight very dissimilar, form a (discontinuous) series of increasing pigmentation and size of eye-ring. This would suggest conspecificity (and the Usambara and Kilimanjaro birds, which look so different, have identical songs—see Appendix 2). Also, with *mbuluensis* as link, the Kilimanjaro *eurycricota* can be regarded as conspecific with the East Kenya *kikuyuensis*.

Certain difficulties have now to be faced. The Usambara birds, just regarded as conspecific with the Kilimanjaro, are, as will be argued below, conspecific with the *stuhlmanni* of Lake Victoria. These are believed to intergrade, through the Yala population, with *jacksoni*. It follows that *jacksoni* would be conspecific with *kikuyuensis*, although, as noted above, the Aberdares situation suggests that they are not. A possible explanation is that here, as in the Great Tits, *Parus major*, of eastern Asia and other examples (Mayr, 1947), we have a meeting of branches of the same species so long separated as to be genetically incompatible.

On the whole, I am prepared to treat all the montane *Zosterops* as conspecific, retaining the names *kulalensis*, *jacksoni* (to cover the whole discontinuous cline from the West Kenya highlands through Laipikia and Gargues to Marsabit and Nyiro), *kikuyuensis* (East Kenya highlands), *silvana* (Teita), *mbuluensis* (including *chyuluensis*, for the arc Mbulu–North Pare), *eurycricota* (Kilimanjaro and outliers), *winifredae* (North Pare), *stierlingi* (Usambara ; see next section). The lowland birds, specifically distinct, are *flavilateralis*, intergrading with *jubaensis* (conspecific with *abyssinica*).

CENTRAL AFRICA

The area dealt with here is a highly mountainous strip about two hundred miles by six hundred, between 38° and 31° E., 3° N. and 6° S., on the eastern edge of the Congo Basin (see Map 7). Here the *Zosterops* show a wide range of variation in size and in general colour of plumage but not in eye-ring, forehead or belly colour. Although they include some of the deepest green birds in Africa, I regard them all as conspecific with the yellow West African *senegalensis*, which in the preceding section was traced south nearly to the Equator.

Zosterops appear to be absent from the centre of the Congo basin 2° N.–5° S., cf. Chapin (1954), but are widespread in the east of it. Topographically this strip is dominated by the western (Albertine) Rift Valley and associated mountains, with the following main features, in succession from north to south : Lake Albert, Ruwenzori (17,000 ft.), Lake Edward, the Kivu volcanos (with forest belts up to over 10,000 ft.), Lake Kivu (at about 5,500ft.), Lake Tanganyika (at about 2,600 ft.). From north-west of Lake Edward to near the head of Lake Tanganyika the highland is continuous at 5,000 ft. or more, but Ruwenzori is isolated from this by the few miles of lower and drier country round Lake Edward. The highlands north-west of Lake Albert are more isolated (and the local *Zosterops* are so little represented in collections that they cannot be discussed). On their west side the Central African highlands decline rapidly into the fully lowland conditions of the Congo Basin with its equatorial forest climate. On the east, however, all the country southwards from Lake Albert, through Uganda and past the shores of Lake Victoria into Tanganyika Territory, lies at nearly 4,000 ft. or over.

In almost the whole of this strip of Central Africa except the flats round Lake Albert the rainfall approaches 60 inches and considerable areas west of Lake Kivu and north-west of Lake Tanganyika, some below 3,000ft., receive over 80 inches. The wettest areas of all are the forested mountains, of which the chief are Ruwenzori and the Kivu volcanos.[1] The vegetation and appearance of the whole area have been graphically described, with photographs, by Chapin (1932).

As previously stated, in Uganda the "yellow" *Zosterops senegalensis* appears to develop into the greener *stuhlmanni* as it approaches the shores of Lake Victoria.

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[1] To the very local high humidity of these mountains the isohyets in Bultot (1950) probably do not do justice.

Here it is a common bird wherever there are trees, at least from about Jinja round the northern and western shores of the lake and thence across western Uganda (but no *Zosterops* seems to have been collected on the other, drier, half of the lake shore). The plumage of *stuhlmanni* is again of a very generalized type—diffuse yellow forehead, medium eye-ring, greenish flanks contrasting with yellow centre of underparts. In fact the only feature that distinguishes these birds from those which are widespread on the mountains of Nyasaland and Tanganyika (and also the Imatong group on the Sudan border) is a certain warm tinge throughout the plumage. Uganda birds from between about 3,700 and 5,000 ft. have wings averaging 58·1, tail/wing ratio 71, dimensions which, like the plumage, are not distinctive.

The *Zosterops* populations of islands in Lake Victoria would repay investigation. The only series is one of twelve kindly obtained for me by Mr. E. G. Rowe on Ukerewe Island, in the south-west of the lake (see Map 6). They have about the same-sized wing (58·8) as the mainland birds just described, but a higher tail-ratio (75), the Ukerewe eye-ring is larger, and the slightly warm tinge is absent from the plumage. In fact, lacking this tinge, in plumage the Ukerewe birds are separable from Imatong mountain birds—and indeed from birds on mountains round Lake Nyasa—only by slightly bigger eye-rings. Again, from Nkosi Is., the most exposed of the Sesse group in the north-west corner of the lake (see Map 7), which is known to have faunal peculiarities (see Pitman, 1929), the single *Zosterops* available has a wing 4 mm. longer than that of any specimen from the opposite mainland and also an abnormally yellow head.

Westwards these *stuhlmanni* extend to the wetter Ruwenzori massif, occupied by *Zosterops* up to at least 9,000 ft., and also to the low hot banks of Lake Albert. Between, there is a narrow corridor, mostly below about 3,000 ft., occupied by the Bwamba forest country (see van Someren and van Someren, 1949), leading north-west across the Semliki into the forested country of the upper Ituri, which declines to about 2,000 ft. In this highly diversified country on the western edge of *stuhlmanni* there is, as would be expected, much variation in *Zosterops*, which has been the subject of great differences in taxonomic opinion. There are adequate series only from Ruwenzori itself and from the upper Ituri (Stockholm Museum) and it is particularly unfortunate that no specimens seem to be known from localities linking the Ituri with the Ekibondo–Garamba area (already referred to under *senegalensis* as showing incipient divergence from that type) and with the smaller and more heavily pigmented birds at Medje, 150 miles to the north and the W.N.W. respectively.

Eighteen birds are available from Bwamba and the low forest country to the west, from Kampi ya Wambuti to Beni, eighty miles to the south, which includes the type-locality of *toroensis*, Kitimba (which is not in present-day Toro). They are, as expected, all small, mean of wings 53·7, tails 36·9.[1] Also as expected, the birds are strongly pigmented, with plenty of both melanin and carotenoid, but they have little yellow on the forehead. On the whole they resemble the Medje birds more than any others and probably they intergrade with them over the intervening "uncollected" country. The Bwamba birds appear to be transitional between those of Uganda on the east (*stuhlmanni*) and the Ituri birds on the west (see Note 19, Appendix 1).

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[1] As Chapin (1954 : 187) has noted, at Nganzi, near Beni, at 3,900 ft. at the western foot of Ruwenzori, he got a male with wing 61 alongside birds of *toroensis* size. The large bird might have been a straggler from the higher slopes.

There has been much difference of taxonomic opinion also about the Ruwenzori birds. I find that specimens from above 5,000 ft. (averaging 6,900 ft.) tend to have a little more melanin in the plumage and to be a little longer in wing and especially in tail than Uganda birds (altitude 4,000 ft.) to the east—wings 56–63 (mean 60·2) against 55–62·5 (mean 58·1), tails 41–49 (mean 44·5) against 37–44 (mean 41·3). (For the Ruwenzori mountain birds some authors have used the name *scotti.*) A series from the western foothills at Mutsora, 4,000 ft., averages the same size as Uganda birds at the same altitude on the east.

In plumage both the higher-altitude Ruwenzori birds and those from the western foothills average a little darker than the Ituri birds (*toroensis*) and also than the Uganda birds. But the Ruwenzori population, with its generally strong melanin and "warm" carotenoid, cannot be separated in plumage from most of the slightly larger birds of Kivu (see below), a hundred miles to the south, on the other side of Lake Edward. In both the Kivu and Ruwenzori populations many of the birds have the melanin of the flanks extending towards the centre and clouding the whole underparts (as in *virens* of South Africa). This does not happen in Uganda birds, but at the same time there are individuals from the mountains that cannot be distinguished in plumage from Ituri or Uganda individuals.

The identity between Kivu and Ruwenzori birds is noteworthy because the birds of the highlands just west of Lake Edward (see also Prigogine, 1953), which form an almost continuous connection above the 1,500 m. contour (approx. 5,000 ft.) between Ruwenzori and Kivu, differ slightly in being purer green, without the "warm" tinge. Moreover within the small area of these highlands, only some fifty miles by seventy, there is striking variation in size of *Zosterops* with altitude. Birds from Lutunguru, on the western edge of the highland, and other localities between 1,400 and 1,500 m. (average 4,700 ft.) have mean of wing 57·1, tail 40·6, while birds from 1,600–2,700 m. (average 6,800 ft.) have wing 61·5, tail 46·6. Moreover the tail/wing ratio of the latter birds is 75 against only 71 for the former series—in accordance with the trend throughout the continent, cf. Part 3. A similar change in dimensions, correlated with altitude, takes place in the Kivu District. Birds from the volcanos average longer-winged and, more markedly, longer-tailed (62·5, 47·9) than those from nearer lake-level (60·9, 45·4).

South-west of Lake Kivu and north-west of Lake Tanganyika lies an area highest in the east, dipping west into the Congo Basin at Kamituga, pioneered by Grauer but recently worked most usefully by Dr. A. Prigogine. The *Zosterops* (described as *reichenowi* Dubois) differ from those of the Lutunguru area, 150 miles to the north, only in having slightly more melanin (perhaps connected with the higher rainfall, 80 against 60 inches). Like them, *reichenowi* lacks the warm tinge characteristic of Ruwenzori and most Kivu birds (as well as *stuhlmanni*) and indeed seems to have less carotenoid than any of the populations mentioned. It may be that further exploration will show a continuous narrow belt of these "colder"-coloured *Zosterops* by-passing the Kivu population on the west (as adumbrated by the fact that Mulungu birds are a trifle greener) and intergrading with the small richly coloured birds of Bwamba–Ituri further north.

The main interest of these southern birds, from Kamituga eastwards, which are all alike in plumage, is the change in their dimensions with altitude in a very short distance. The high-level birds, round about 7,000 ft., in the Muusi neighbourhood, are practically the same size as those at 6,800 ft. in the highlands west of Lake Edward—wings averaging 61·4, tails 45·3. But only forty miles to the west, round Kakanda–Kulundu, at 4,000 ft., the averages drop to 55·9 and 39·1 ; and twenty miles west again, round Kamituga and Utu, at about 3000 ft. (here the floor of the Congo Basin), the birds are smaller still, with wings only 53·1, tails 35·5. Further, a few geographically intermediate specimens fall perfectly on this size-cline.

Summary

While all the birds are regarded as conspecific with *senegalensis*, it seems worth while to retain the name *toroensis* for the small lowland birds N.W. of Ruwenzori and *reichenowi* for the " cold " green birds of the area N.W. of Lake Tanganyika. Ruwenzori and Kivu mountain birds are regarded as transitional between *stuhlmanni* of Uganda and *reichenowi*. Local variation in dimensions is great but consistent. It cannot be recognized nomenclatorially.

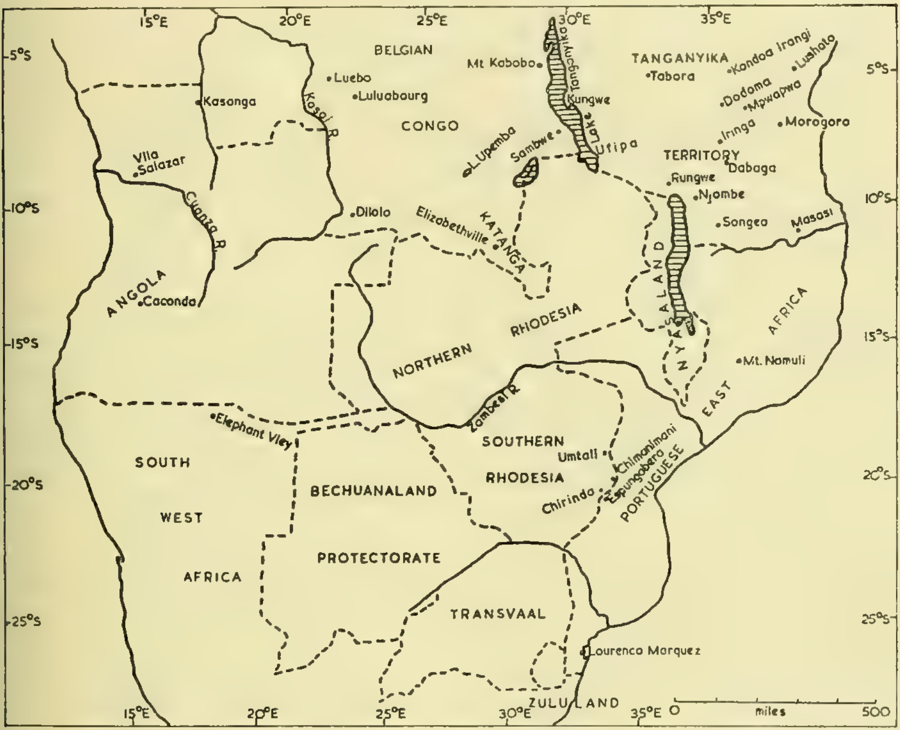
SOUTHERN TROPICAL AFRICA

This area (Map 8) extends from the southern limits of those dealt with in previous sections to the borders of South Africa. It contains a number of poorly differentiated *Zosterops* populations which differ in little but intensity of melanin, but have been allocated to one or other of two species on this criterion.

I believe that this distinction cannot be maintained except for the lowland, dry-country form, *flavilateralis*, which extends south from Kenya, in a strip through the middle of Tanganyika to about as far as the line Tabora–Morogoro. Between Tabora and Lake Victoria *Zosterops* seem to be absent ; and in southern Tanganyika *Zosterops* appear to be purely montane except for rare occurrences in the south-east (see Note 13, Appendix 1).

The material of *flavilateralis* from Tanganyika does not suffice to define the local variation fully, but specimens from the moister country of Kondoa, Morogoro (Uluguru) and Usambara tend to be particularly green. They show in fact so much convergence towards the highland (forest-edge) birds of Uluguru and Usambara that some skins are not at first sight easy to allocate—even though the *flavilateralis* prove to have (B) melanization and the montane birds (A). The possibility of hybridization, for example at Lushoto (4,000 ft., Usambara) and Kibungo (700 ft. eastern foot of Ulugurus) whence particularly " difficult " skins come, cannot be excluded. However, I believe the best course is to regard these highland and lowland forms as belonging to different species.

Turning now to the Congo Basin, it appears, as already noted, that as far south as about 5° S. no *Zosterops* have been collected in the space of nearly 400 miles, between Luluabourg (in the Kasai country of the south-west) and the foot-hills of the mountains overlooking Lake Tanganyika in the east, or, to the south-west, Upemba (Map 8). But between the Kasai and the Transvaal, and from Angola to the Indian Ocean, *Zosterops* with variable, but never highly distinctive, features are generally distributed. Some of them cannot be differentiated from the birds of the Imatong group of mountains far away on the Sudan–Uganda border, others differ from birds on the north and west of Lake Victoria only in slightly less "warmth" of tone, others again can be matched by abnormal West African individuals, others are extremely like the richly pigmented birds of Kivu and still others cannot be separated on plumage from individual South African birds.


15°E
20°E
25°E
30°E
35°E
5°S
10°S
15°S
20°S
25°S
BELGIAN
CONGO
Luebo
Luluabourg
Kasonga
Kasai R.
Mt Kabobo
Lake Tanganyika
Kungwe
Ufipa
Sambwe
L. Upemba
TANGANYIKA
TERRITORY
Tabora
Kondoa Irangi
Lushoto
Dodoma
Mpwapwa
Morogoro
Iringa
Dabaga
Rungwe
Njombe
Songea
Masasi
Vila Salazar
Cuanza R.
ANGOLA
Caconda
Dilolo
Elizabethville
KATANGA
NYASALAND
NORTHERN
RHODESIA
EAST
AFRICA
Mt. Namuli
Zambezi R.
SOUTHERN
RHODESIA
Umtali
Chimanimani
Vumba
Chirinda
PORTUGUESE
Elephant Vley
SOUTH
WEST
AFRICA
BECHUANALAND
PROTECTORATE
TRANSVAAL
Lourenco Marquez
ZULULAND
0
miles
500

MAP 8. Southern Tropical Africa.

Taken as a whole, these southern tropical birds range in general colour of plumage from predominantly yellow to predominantly green, and as there is a complete gradation the attempt to divide the populations between the species on this criterion alone, as is usually done, leads to difficulty. In dimensions all the populations, irrespective of colour, form one group of tail/wing ratios and beak/wing ratios (Text-figs. 4 and 8) and also when tail/wing ratios are plotted against altitude and against minimum temperatures (Text-figs. 6 and 7). (In the whole group of populations the tail/wing ratio is unusually constant in the face of changes in altitude and temperature, and so is the beak-length with changing wing-length.) The main point for the taxonomist is that analyses of dimensions give no support to the view that more than one species of *Zosterops* is present in the area under discussion. This view meets, however, with some difficulties on geographical and ecological grounds.

Dark populations are always, and dark individuals are nearly always, found at higher altitudes and where evergreen forest occurs, while the yellower birds usually occur in drier and lower country, dominated by deciduous woodland. But this ecological distinction is far from invariable. For example, R. H. Smithers has noted (*in litt.*) yellow birds in Southern Rhodesia in both "thorn veld" and evergreen growth, and Benson (1946*a*) has obtained such birds in the evergreen forest at Vumba (near Umtali, 5,000 ft.). Swynnerton, as his labels show, has collected yellow birds in the Chirinda and Chipete forests, but a dark bird in the Chimanimani evergreen bush half-way between these two localities. Again, some individuals on the border of Northern Rhodesia and the south-eastern Congo (Katanga) are so green that some workers have allocated them to *virens* (see Note 20, Appendix 1)—there are no mountains in the area, but some patches of evergreen growth too extensive to be called riparian (C. W. Benson *in litt.*). One is reminded of the dark individuals, formerly regarded as a separate form, *phyllica*, that crop up in the Bamenda highlands (see p. 354).

Lynes (1933) collected both yellower and greener birds (which he attributed to different species) in the same situations, the "edges of the forest-jungles" at 6,500 ft. in the Njombe District of Tanganyika Territory. Moreover, the *Zosterops* of the Kungwe–Mahari mountains, on the east shore of Lake Tanganyika, are associated with evergreen forest (about 6,000 ft. upwards), yet when laid out with a long series of specimens from southern tropical Africa they fall into the yellower half. In Nyasaland the relict forest on some mountain tops (Mangoche, Dedza, Chongoni and Nchisi) is occupied by birds as yellow as those of the Rhodesian savannas, but greener birds occupy Mlanje, Cholo, Soche, Zomba, Ndirande and (greenest of all) Nyankhowa and the Nyika Plateau (Benson, 1945, 1953). No adequate meteorological data exist, but Benson (*in litt.*) is satisfied from his local experience that the mountains of the first group have a lower rainfall than the others. In none of the mountain forests where green birds have been collected has it been proved that a transition from yellower to greener birds takes place as the mountain is ascended and evergreen forest becomes the dominant vegetation ; and there seems no proof that yellow and green birds associate together. There is in fact no indication of such local clinal variation as previously noted on the slopes of the Imatong mountain group and elsewhere over more level country with a rapidly changing rainfall, as in Sierra

Leone. The Nyasaland situation suggests at first the possibility that here we have ecological replacement of one species by another as in the instances given by Moreau (1948). For example, an isolated mountain forest, from which the typical montane woodpeckers (*Mesopicos* and *Campethera*) are absent, is inhabited by a species of *Yungipicus* that elsewhere is a savanna bird. Moreover, as will be shown in the next section ("South Africa"), a few hundred miles to the south-east of Nyasaland, in Zululand and southern Portuguese East Africa, yellow birds that are undoubtedly conspecific with, and have a distribution continuous with, those of Nyasaland appear to live as "good species" alongside, but ecologically separated from, green South African birds.

These last closely resemble some of the darkest Nyasaland birds in plumage, but they differ from the Zululand yellow birds and from all the Nyasaland birds, both the yellow and the green, in having a higher tail/wing ratio, 75 against 67–71. Here we come up against the question of the value of this ratio as a taxonomic character (Part 3). On the other hand, as noted above, the yellow and the green birds of Nyasaland (and elsewhere in southern tropical Africa) do not differ in bodily proportions. It is a curious fact, however, that the dark birds tend to be unexpectedly small for the altitudes at which they are found. In particular, the dark Nyasaland birds (No. 64 in Appendix 3) have the same mean wing-length, 58·5 mm., as the local yellow birds (No. 63), with an average altitude 2,000 ft. lower and a climate certainly warmer. This is, of course, contrary to the trend otherwise general throughout Africa—and beyond—as discussed in Part 3.

Thus arguments can be adduced for regarding the yellower and the greener birds in at least part of southern tropical Africa as belonging to two different species. Against this are the complete gradation that can be made up from birds from different localities and the fact that Benson (1953), who has an unrivalled knowledge of both forms in Nyasaland, can find no difference in their habits and their calls. On the whole it seems preferable to regard all the *Zosterops* of southern tropical Africa as belonging to the same species.

The most north-westerly population in southern tropical Africa, namely, that in the Kasai district of the south-western Belgian Congo (*kasaica*), is the most distinctive. They are the first *Zosterops* encountered after crossing the great forest from the north. The series from about 4° 30′ S., round Luebo and Luluabourg, consists of very small short-tailed birds (wing 52·5, tail 35·1), which conforms with their low altitude (*ca.* 2,000 ft. a.s.l.) and high minimum temperature (64° F.). On the whole they are more like the little Medje birds 700 miles away to the north-east, on the other side of the Congo Basin, than any others in Africa, but they are rather more olive throughout, with very narrow eye-rings and no clear yellow on the forehead at all. They occupy country that, with an annual rainfall around 60 inches, is not so wet as that of Medje, but nevertheless the resemblance between these two populations, sundered by the forest, may be due to convergent evolution in similar equable climates, rather than to recent common ancestry. It is possible that a narrow belt of small birds remains to be discovered running eastwards from Luluabourg along the southern edge of the Congo Forest to intergrade clinally with the equally small, but greener, birds known from Kamituga (referred to in the section on Central Africa) at the foot of the eastern rim—themselves probably intergrading clinally to Medje.

Towards the south-west, *kasaica* apparently extends at least to the north-eastern border of Angola—cf. the one imperfect specimen from Kasanga on the Kwango (Cuango) river. Thence, there is almost certainly intergradation with the birds of the highlands in the centre of Angola, which are much larger and much duller in plumage. The few specimens available from the intervening area Ndala Tando (= Vila Salazar)–Quicolungo–Canhoca (see Map 9), which is rather higher and drier country than that inhabited by *kasaica*, are already duller in plumage and much larger (wing 57·2, tail 39·0).

Another 150 miles intervene to the south before another series of *Zosterops* is available from central Angola (Benguela Highlands) at 4,500 ft. upwards (Note 21, Appendix 3). This area has the highest rainfall in Angola[1] and it is therefore unexpected that the birds there (described as *quanzae*) are all duller in plumage than the Vila Salazar series. This may be connected with the fact that the Vila Salazar area is one of semi-evergreen forest (dominants *Albizzia*, *Celtis* and *Ficus* spp.), while the Benguela highlands, though having a higher rainfall, are occupied by savanna with much (deciduous) *Brachystegia* (Gossweiler and Mendonça, 1939), and with evergreen forest only in gullies (C. M. N. White *in litt.*).

Also, the birds of the Benguela highlands are much larger (wing 61·8) than those round Vila Salazar and in fact are the largest in southern tropical Africa (see Nos. 56 *et seq.* in Appendix 3), although they come from an average altitude of only 5,500 ft. The explanation is presumably that, as data from ten local meteorological stations show, these birds experience abnormally low minima, averaging only 45° F. in the cool season—cf. the general size/temperature regression in Part 3. These large pale birds extend south-east at least to Vila Ponte (wing 64), but further down the Cubango (Rio Mbale) a specimen, though pale, is within the Rhodesian size-range (wing 58).

Further collecting may bridge the present gap in *Zosterops* distribution in this part of Africa—nearly 400 miles to Dilolo in the east and 200 to Elephant Vley in the south—and show whether, as expected, there is a transition to the rather yellower and smaller birds (*anderssoni*) that occupy so much of the remainder of southern tropical Africa. There is at present no evidence that any such *Zosterops* occur further west in Angola, to the Atlantic, or further south in South West Africa, except along the northern border, or in Bechuanaland, but very similar birds are distributed through the Rhodesias, Nyasaland and Portuguese East Africa, right to the Indian Ocean, and also northwards in the south-eastern Belgian Congo to at least 8° S. The whole of this great area is, as already indicated, dominated by

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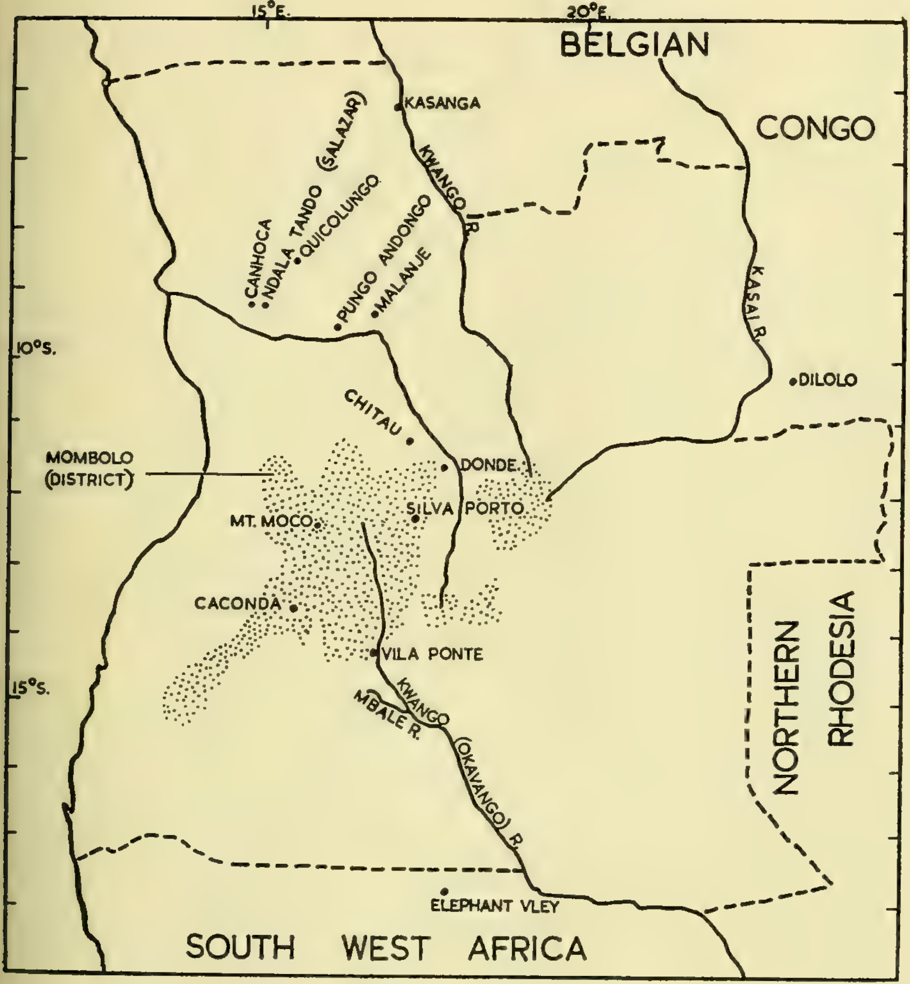
[1] Cf. the isohyets in the *Atlas de Portugal Ultramarino* (Lisboa, 1948). They differ much in detail from those in Gossweiler and Mendonça (1939), but since they are presumably based on more data they are taken to be more nearly correct. As so often in climatological maps, the isohyets have had to be sketched in the Atlas from the records of widely scattered stations and it seems that in drawing them advantage has not been taken of the guidance orography can give. However, the main trends of the isohyets are no doubt somewhere near the truth.


15°E.
20°E.
BELGIAN
CONGO
KASANGA
CANHOCA
NDALA TANDO (SALAZAR)
QUICOLUNGO
PUNGO ANDONGO
MALANJE
KWANGO R.
KASAI R.
DILOLO
10°S.
CHITAU
DONDE
MOMBOLO (DISTRICT)
SILVA PORTO
MT. MOCO
CACONDA
VILA PONTE
15°S.
KWANGO
MBALE R.
(OKAVANGO) R.
NORTHERN RHODESIA
ELEPHANT VLEY
SOUTH WEST AFRICA

Areas above 1,500 m. dotted.

MAP 9. Angola.

deciduous woodland, though patches of evergreen forest occur, especially on the highest points.

The yellowest populations of all are the most westerly, in western Northern Rhodesia. Equally yellow individuals occur as far east as Nyasaland (even at 6,000 ft. on the Nyika plateau), but most of the specimens from east of about 29° E. are a trifle greener than those from further west. The most easterly of all, in southern Portuguese East Africa (Mozambique), Zululand and the low-veld of the north-eastern Transvaal average a trifle greener still. Northwards through Portuguese East Africa it appears that the *Zosterops* generally become a trifle more richly pigmented, especially golden, a character that is best marked (but still only visible when series are compared) in the birds of the Songea highlands on the north-east side of Lake Nyasa. As the single bird collected between there and Indian Ocean, in the lowlands at Masasi, shows the same character, it may be that there is a continuous, though extremely sparse, population over much of south-eastern Tanganyika Territory. These brightly coloured birds of south-eastern Tanganyika can, however, be matched by individuals from Nyasaland and Northern Rhodesia. Whether such birds extend far enough north to come in contact with the pale *flavilateralis*, hitherto not recorded south of the line Morogoro–Tabora, is unknown : and it would be interesting to know their relationships if they do so.

In size the "yellow" populations of the Rhodesias, Nyasaland and also the south-eastern Congo, all around 4,000 ft., are remarkably constant, varying only from 58·6 to 59·9 mm. in average wing and from 39·8 to 42·0 in tail (Nos. 59, 60, 62, 63 in Appendix 3). A series from around 5,800 ft. in N. Rhodesia (No. 61) averages, as expected, larger (wing 61 mm., tail 42·5). By contrast, but again in accord with expectation, the birds from the coastal belt (below 1,000 ft.) along the Indian Ocean average only 56·6 mm. in wing and 39·2 in tail (No. 65).

Returning to Northern Rhodesia, the variation in the *Zosterops* may now be traced north through the south-eastern Belgian Congo (Katanga). About 200 miles north of the territorial border, in the wooded savanna of the Upemba National Park (*ca.* 8° S. ; altitudes 4,500 ft.–6,000 ft.) the birds are duller, apparently with a little more melanin and a little less carotenoid. In this they resemble the birds from the central Angola highlands (in fact Verheyen (1953) has used the same name, *quanzae*, for them), but they are smaller—wing 59·9 against 61·8. Similar populations occur on the west shore of Lake Tanganyika at Sambwe and Kabobo, the latter rather darker. Although there are great gaps east and west of Upemba, from which no specimens are known, it appears that we have a cline from the yellower birds (*anderssoni*) of the Rhodesias and Katanga, northwards through a stage deficient in both pigments to the deep green birds, with much melanin, in the highlands north-west of Lake Tanganyika (*reichenowi*—see section on " Central Africa "). It is curious that, as already mentioned, on the Kungwe mountains just across Lake Tanganyika the *Zosterops* are decidedly yellow.

Turning now to the dark birds, the most richly pigmented of all are those inhabiting the Rungwe and Poroto Mts. at the north end of Lake Nyasa (see Note 22, Appendix 3), a small area that, with one station registering 100 inches a year, is about the wettest in southern tropical Africa. A few miles to the south, on the Nyika, Nyankhowa and Masuku Mts. of northern Nyasaland, the birds are nearly as richly coloured, with dark green flanks contrasting with the strong yellow centre of the underparts ; but on the other Nyasaland mountains, further to the south, none of the birds are so deeply pigmented and, as already noted, some are actually yellow.

Facing the Poroto birds on the west, over 100 miles away across the Rukwa depression, the nearest montane *Zosterops* are those of the Ufipa highlands, and they, like those of the Kungwe–Mahari Mts., further north up the east side of Lake Tanganyika, are, as mentioned above, yellower. But eastwards and northwards from Rungwe the highlands are continuous to Njombe and Iringa, and all the *Zosterops* are dark, with a local variation that has greatly bothered taxonomists. It now appears that the birds on the average darkest, and most nearly resembling those of Rungwe, come from round Dabaga, on the top of the humid Uzungwe scarp that forms the seaward edge of the Iringa highlands. The birds that average next darkest are those of Njombe, while those from Iringa itself, which is not so high and humid as Dabaga and Njombe, are a little yellower. (For the nomenclatorial difficulties concerned see Note 23, Appendix 3.)

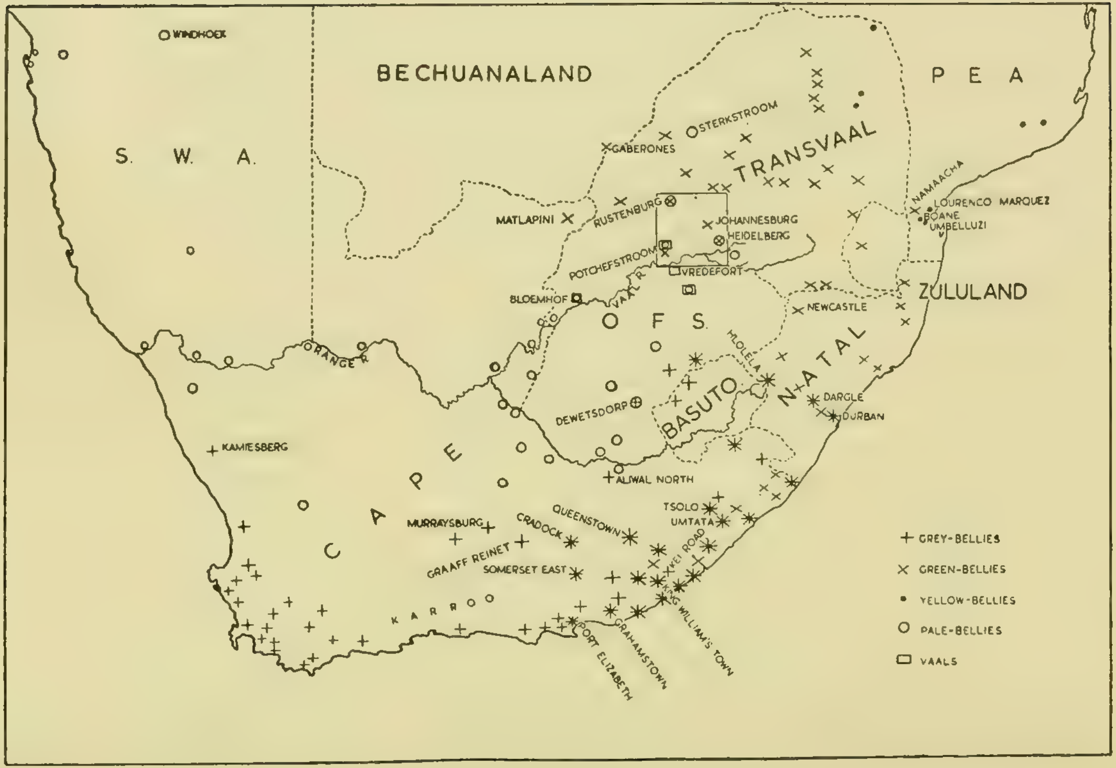
Birds coloured like those of Iringa occupy the isolated mountains further north—Kiboriani, the Ngurus, Ulugurus and Usambaras—getting smaller as the altitude and latitude decrease and the minimum temperatures rise (populations 68–72, Appendix 3). As previously noted, the *Zosterops* of these Tanganyika mountains are partly islanded in the small, generally paler, *Zosterops* of the surrounding savanna which tend to converge in colour. These lowland birds to some extent penetrate the highlands—for example, reaching at least 4,000 ft. in the cultivated areas in the middle of the West Usambara plateau—but there is no evidence that the highland birds ever enter the lowland savanna.

Summary

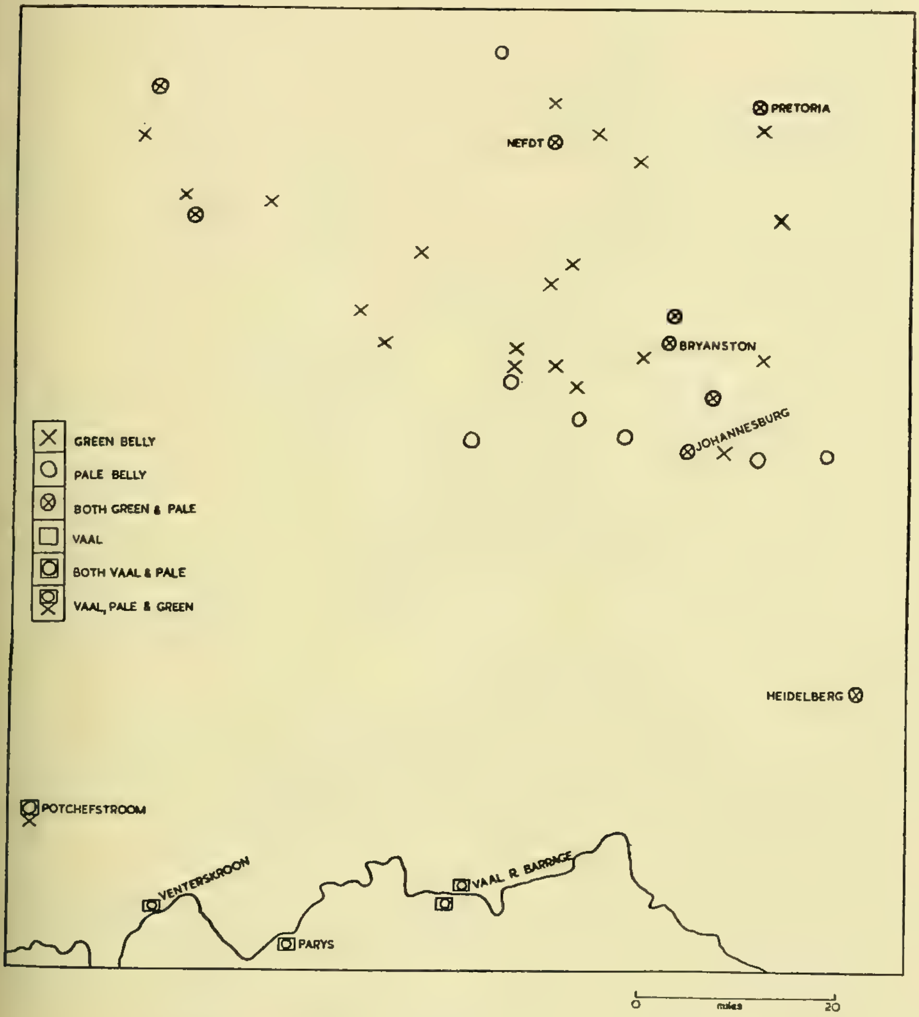
The whole of the *Zosterops* inhabiting southern tropical Africa are regarded as belonging to the same species, *senegalensis*. It may be useful to retain the following subspecific names : *kasaica* for the small olive birds of the south-west Belgian Congo ; *quanzae* for the large dull birds of Central Angola ; *anderssoni* for the yellow birds from Northern Rhodesia to the Indian Ocean ; and *stierlingi* for the more richly pigmented birds of the Nyasaland and Tanganyika highlands. But the ranges of the last three cannot satisfactorily be delimited because intermediate populations are so prevalent and similar birds appear discontinuously, perhaps as a climatic response (convergence).

SOUTH AFRICA

It would have been impossible to write even the present tentative account without much co-operation from ornithologists in South Africa, where I am especially indebted to Mr. C. J. Skead for the Cape Province data and to Dr. R. M. Harwin for mapping the Transvaal situation.


WINDHOEK
S. W. A.
BECHUANALAND
P E A
GABERONES
OSTERKSTROOM
TRANSVAAL
MATLAPINI
RUSTENBURG
JOHANNESBURG
HEIDELBERG
POTCHEFSTROOM
VREDEFORT
BLOEMHOF
VAAL R.
NAMAACHA
LOURENCO MARQUEZ
BOANE
UMBELLUZI
ZULULAND
NEWCASTLE
O F S.
HLOLELA
NATAL
DARGLE
DURBAN
BASUTO
DEWETSDORP
ORANGE R.
KAMIESBERG
CAPE
ALIWAL NORTH
TSOLO
UMTATA
QUEENSTOWN
CRADOCK
MURRAYSBURG
GRAAFF REINET
SOMERSET EAST
KEI ROAD
KING WILLIAM'S TOWN
GRAHAMSTOWN
PORT ELIZABETH
KARROO
+ GREY-BELLIES
× GREEN-BELLIES
• YELLOW-BELLIES
○ PALE-BELLIES
□ VAALS

MAP 10. *Zosterops* distribution in South Africa.


PRETORIA
NEFDT
BRYANSTON
JOHANNESBURG
GREEN BELLY
PALE BELLY
BOTH GREEN & PALE
VAAL
BOTH VAAL & PALE
VAAL, PALE & GREEN
HEIDELBERG
POTCHEFSTROOM
VENTERSKROON
VAAL R BARRAGE
PARYS
0
miles
20

MAP 11. *Zosterops* distribution in the southern Transvaal.

South of the Zambesi there are five main colour-forms of *Zosterops*, which have always been regarded as belonging to at least four different species. Their ranges and main characters are given in Maps 10 and 11 and Table 2 (see also Note 24, Appendix 1). For clarity the five forms are referred to in this discussion as "grey-bellies," "pale-bellies", "Vaals", "green-bellies" and "yellow-bellies". Briefly, grey-bellies differ from green-bellies only in lacking yellow pigment on the belly, but from pale bellies in deeper pigmentation of upper as well as under parts and in other characters. Vaals differ from pale-bellies only in having yellow throughout their underparts. Green-bellies differ from yellow-bellies (the *anderssoni* already discussed under "Southern Tropical Africa") in having more melanin throughout and individuals of them can be matched in colour with birds from the mountains of Nyasaland. All the purely South African forms have a high tail/wing ratio (75–79), contrasting with under 70 for the yellow-belly (*anderssoni*) that enters from the north.

TABLE 2.—*The main Characters and Distribution of South African* Zosterops.

N.B.—The subspecific names usually applied are inserted in brackets.

	Belly colour.	Main area.	Upper parts.
(1)	Grey (*capensis*[1] and *atmorii*) . .	Cape Province and Basutoland .	Green
(2)	Whitish with chestnut wash on flanks (*pallida*)	Orange River Basin .	Paler and greyer
(3)	Pale yellow with chestnut wash on flanks (*vaalensis*)	Along lower Vaal R. (all localities shared with *pallida*) .	As (2)
(4)	Green, yellowish in middle (*virens*) .	Eastern Cape, Natal, Zululand, Transvaal .	As (1)
(5)	Yellow, green wash on flanks (*anderssoni*)	Zululand and N.E. Transvaal . (thence northwards)	Yellower than (1)–(4)

[1] The most westerly grey-bellies (" *capensis* ") differ from all the others in this table in lacking any yellow over the lores (or over base of upper mandible).

In South Africa the *Zosterops* arrangement differs from that elsewhere in Africa in that the colour-forms show considerable geographical overlap and even more ecological. All are limited to places where there are trees ; but, given that essential, they show a breadth of habitat tolerance that is unusual in African birds and is great enough to make it difficult to be sure what their original vegetational associations were.

(*a*) The grey-bellies occur from sea-level to over 7,000 ft. (Drakensberg). They inhabit all sorts of tree-growth, from the patches in the extremely dry Kamiesberg (south-east of the mouth of the Orange River) to the Knysna and Hogsback evergreen forests, including gardens and plantations of pine and eucalyptus (Skead).

(*b*) Green-bellies are usually referred to as predominantly forest birds but, with as big an altitude-range as the grey-bellies and a wider geographical range, they inhabit if anything an even greater variety of arboreal vegetation—the coastal forests of the Eastern Cape, Natal and Zululand, the acacia-veld of the Natal uplands, the dry Transvaal high-veld, the gardens of Johannesburg and even the taller " bush " in the east of the Bechuanaland Protectorate.

(*c*) Yellow-bellies are limited to the " low-veld ", the deciduous and pyrophytic " bush " of the eastern Transvaal, Zululand, and Portuguese East Africa, thence spreading north and west across the Rhodesias.

(*d*) Pale-bellies inhabit the southern half of South West Africa, the south-western Transvaal, the northern Cape and the whole of the Orange Free State—much of their area averaging less than 10 inches of rain a year. In the driest parts the birds seem to occur only in the valleys (especially along the Orange River), where there is some water, artificial or other (but there is no record of the birds drinking).

(*e*) Vaal *Zosterops* are known only from localities on and near a short stretch of the lower Vaal River, from all of which pale-bellies are also known.

As will be seen from Map 6, while *Zosterops* are generally distributed in South Africa, there are two areas where they seem at most very sporadic, (i) a wide belt in the western Cape Province from the Karroo northwards and (ii) most of South West Africa and the Bechuanaland Protectorate. The necessary trees exist scattered over much of the second area, but not in the Karroo.

Local Variation

Size generally

As shown in Appendix 3 (populations 73–80), in each colour-type wings average longer in the cooler and/or higher areas, except that the green-bellies of the Natal–Cape lowlands average no larger than the Zululand birds that inhabit a slightly warmer climate (but by only about 2° F.).

Grey-bellies

East of about Port Elizabeth the grey-bellies average slightly yellower on the upper parts and throat and have some yellow on the forehead and lores. (This last feature corresponds with the amount of yellow on the heads of the green-belly population with which they interbreed—see below.) Enough specimens are not available, but the transition from the western form (*capensis*) to the slightly yellower eastern form (*atmorii*) appears to take place in a zone including Murraysburg, Graaff Reinet and Port Elizabeth, from all of which the specimens are intermediate in character.

Well to the north-west of any other specimens of *capensis* two from the dry Kamiesberg are slightly duller above than other *capensis* and have flanks slightly redder. Both these features of their plumage adumbrate the characters of the pale-bellies, which are known from about seventy miles away on the north. However, something similar is shown by northern representatives of *atmorii*, further to the east, near Aliwal North (kindly communicated by Mr. P. A. Clancey). The plumage of these birds (and of one from Dewetsdorp) is duller throughout than that of the *atmorii* nearer the coast. On the flanks, however, these birds are a particularly pure grey, with no reddish, so that they can hardly owe their general divergence from typical *atmorii* to an infusion of the local pale-belly characters. On the contrary, the dullness of the plumage appears to be correlated with the drier climate, for Dr. Auber has ascertained that a Kamiesberg *capensis* contains a lower proportion of (A) melanin and more (B) than a specimen from the more humid Knysna (see Part 2).

Green-bellies

These show much individual variation. Exceptionally dull specimens are scattered throughout the range, but every specimen from the driest part of the range (western Transvaal and eastern Bechuanaland—Note 25, Appendix 1) is slightly pale and dull, with the same divergence from the typical appearance as mentioned above for the dry-country representatives of *capensis* and *atmorii*. Moreover, the dull specimen (from Rustenburg) that has been tested shows a predominance of (B) melanin in contrast to the predominance of (A) melanin in a specimen from a humid Natal habitat (Dr. Auber).

Pale-bellies

Apart from size, no consistent local variation can be established, but the individual variation is very high. Besides occasional faint suffusion of yellow on the underparts, some specimens have the whole area between throat and vent nearly white, others almost entirely rufous. One from near Rustenburg, on the edge of the pale-belly range and some 250 miles from the nearest grey-bellies, has the underparts so grey that it would, if found south of the Orange River, probably have been cited as a hybrid *atmorii* × *pallida*. The occurrence of such a specimen, which must be of pure pale-belly stock, is important to bear in mind when considering another highly abnormal bird, shot at Dewetsdorp in the Orange Free State out of a flock composed partly of grey-bellies. This individual (Kaffrarian Mus. B2863) is predominantly warm russet below, becoming almost grey on the chest—a putative hybrid (see also Note 26, Appendix 1).

General

It will be observed that each of the colour-forms of extensive range in South Africa varies geographically in the same way. Each has its largest individuals in the coolest areas and its dry-country outliers less saturated in colour than the main populations in less arid climates. It is noteworthy that this consistent agreement with Bergmann's and Gloger's rules takes place within what are generally accepted as individual subspecies ; and the agreement with Gloger's holds good in the actual type of melanization so far as this has been tested.

Overlap and Relationships of the Colour-forms

Grey-bellies and green-bellies

As shown in Map 10, there is a great overlap in the geographical distribution of these birds and, as already mentioned, no distinction in their habitat-preferences (or other behaviour). Some information (collated by Mr. Skead) is also available about their relative abundance in different localities. It can be only in general terms because colour of belly is difficult to see in such small restless birds and a formal census in an area where both occur is impossible.

In the narrow belt about King William's Town, where grey- and green-bellies commonly interbreed (see below), they appear to be about equal in numbers. Westwards green-bellies diminish rapidly: at Queenstown, Somerset East and Cradock they are much in the minority, at Grahamstown and Port Elizabeth (less than 150 miles from King William's Town) they are rare, and further west they are unknown. East of King William's Town the grey-bellies at first fall off rapidly, and green-bellies predominate heavily around Butterworth, Tsolo and Umtata, but further north, at the higher altitudes, in and on the borders of Basutoland, the two forms seem equally common again. Thus grey-bellies reassert themselves, as it were, in Basutoland and on the Natal slopes of the Drakensberg after apparently being somewhat eclipsed by green-bellies nearer the coast on the south. In coastal Natal greys are rare, being known only from two specimens (Dargle and Durban—nearly 400 miles east of King William's Town). It is difficult to interpret these occurrences. The Durban specimen is too small to be a wanderer from the Basutoland population and, if a straggler, must have come along the coast from the south-west.

Since Mr. Skead's field observations first suggested the relationships between the grey-bellies and the green-bellies he and his helpers have tried to record belly colour in every case of birds with nests or dependent young. The following results are all derived from the area King William's Town–Kei Road, where the two forms are constantly seen in the closest association:

(1) Grey + green sharing incubation (of 3 eggs later destroyed).
(2) Grey + green with fledglings (belly-colour not ascertainable).
(3) Grey + green feeding one grey fledgling.
(4) Grey + green with one grey fledgling.
(5) Grey + green feeding three green nestlings.
(6) Grey + green ,, three grey fledglings.
(7) Green + green ,, three grey fledglings.
(8) Green + green with three green fledglings.
(9) Green + ? feeding three grey fledglings.
(10) Green + ? ,, grey fledglings (? number).
(11) Green + ? ,, one green fledgling.

(In cases (9), (10) and (11) the second parent was not observed.)

The above data are somewhat conflicting and the record that each bird, both parent and fledgling, is a typical green-belly or a typical grey-belly must be accepted subject to the fact that, as noted in Part 2, only a proportion of intermediates is obvious to the eye. (Indeed this happens even in field observations on the Carrion and Hoodie Crows—Mayr, 1947.) One "good" example of an intermediate *Zosterops* has recently been collected by Skead; its definitely grey flanks are separated by as marked yellow down the middle of the belly as ever occurs in the green-flanked type. Two other specimens from King William's Town and Newcastle have the flanks so dull greyish a green that they look somewhat intermediate.

One definite conclusion from the field data given above is that the two green-bellied parents in (7) must have been heterozygous and that their fertility was normal, but no other genetical inferences can safely be drawn. Nor is the taxonomic problem settled. Bearing in mind also the geographical distribution, it seems that the grey-bellies and the green-bellies cannot be merely colour-phases. If the belt of interbreeding of the two colour-types is really as narrow as that covered by the limited field-observations, then there might be a case for treating the two birds as species analogous to the Carrion and Hoodie Crows, but on the whole for the present they are best regarded as subspecifically related.

Pale-bellies and grey-bellies

Pale-bellies differ from the other South African *Zosterops* in having less saturated coloration—grey-green upper parts, paler yellow and wholly (B) melanin—presumably correlated with their drier environment. Their beaks tend to be more slender towards the tip, and in voice they differ slightly from both grey-bellies and green-bellies, which are alike. More important, their dimensions are peculiar in that their wings are abnormally short in relation to the low temperatures they experience (Part 3), though they share the high tail/wing ratio of other South African *Zosterops*.

As will be seen from Map 10, in most of the area where pale-bellies and grey-bellies might be expected to overlap, i.e. in the south-western Cape Province, *Zosterops* of any sort have been very little recorded. The two forms have been collected together in only one locality, Dewetsdorp in the Orange Free State (out of the same flock ; Kaffrarian Museum), and the two specimens concerned each show a slight approach to the plumage characters of the other. The only other locality where the two forms have been found close together is Aliwal North (7 miles apart ; Mr. P. A. Clancey). As already noted, all the most northerly grey-bellies—those nearest to the pale-belly range—diverge slightly from the typical in the direction of pale-belly characters, but they can hardly be accepted as hybrids. Moreover, colour is not the only character separating the two types.

Pale-bellies and Vaals

Vaals are known only from the banks of the last 200 miles of the Vaal River and up to about thirty miles on either side (at Potchefstroom, Vredefort and perhaps Heidelberg), in localities where pale-bellies are recorded at the same season of the year, and mixed flocks are reported. The area has no notable ecological peculiarities (Dr. E. A. C. L. E. Schelpe *in litt.*). The relative abundance of the two forms would be impossible to assess reliably in the field. No biological information has been recorded about Vaals except by Plowes (1946 and *in litt.*) ; and it may be doubted whether any significant differences exist.

Vaals have always been regarded as a distinct species (*Z. vaalensis*), but the five I have examined (only six specimens seem to exist in museums) show only one consistent difference from pale-bellies—they have a strong suffusion of yellow all over the underparts, which gives them a brighter yellow throat and a yellow belly with an isabelline, rather than a chestnut, wash on the flanks. Bearing in mind also the geography, specific separation seems unjustified and this is clinched by the existence of somewhat intermediate specimens. Two with slight yellow wash on a portion of the underparts come from Venterskroon and Bloemhof (Transvaal Museum) and one with yellow wash over the whole underparts from Rustenberg—100 miles from the Vaal.

On the whole it seems best to regard "*vaalensis*" as a localized xanthochroic variety of *pallida*. Comparable cases are known. For example, the grass-warbler *Cisticola juncidis*, which has a vast range, from Spain to Australia and Natal, produces in a few square miles at the north end of Pemba Island, and apparently nowhere else, an erythristic form that interbreeds with typical birds (Pakenham, 1937).

Pale-bellies and green-bellies

These two forms overlap in the southern Transvaal to the extent shown in Map 11. Critical information as to the extent to which they associate together in flocks, or interbreed, is lacking, but at Bryanston and at Hartebeestepoort both have been found in the breeding season. North of a line through Johannesburg greens occur, and apparently predominate, right into the dry country of the west, at least to Gaberones, over the Bechuanaland border, and the sources of the Great Marico, with one locality of pale-bellies interpolated—Sterkstroom (Transvaal Museum). The furthest extension of green-bellies south-westwards is at Potchefstroom, where both pale-bellies and Vaals also occur. There is no indication of inter-breeding anywhere.

Green-bellies and yellow-bellies

At the northern end of their range the green birds from South Africa overlap the yellow birds of southern tropical Africa (*anderssoni*) in Zululand and the adjacent north-eastern Transvaal. This is the only case in South Africa where there is evidence of decisive ecological separation between two forms. In Zululand the green birds are said to be confined to patches of evergreen forest in the coastal acacia "bush" and to the forest on the Lebombo Hills (which do not exceed about 2,000 ft.), while the yellows occupy the surrounding more open vegetation (Mr. J. Vincent *in litt.*). It would be interesting to know whether the yellows and greens actually meet or associate anywhere, as, for example, the grey-bellies and green-bellies do constantly in the Cape Province.

All the Zululand specimens available are either typical yellows or typical greens; and it is important to remember that there is a difference in dimensions as well as in amount of melanin. The yellows average about 3 mm. shorter in wing than the greens and their tail/wing ratio is only 69 compared with 75 in the greens (and 75–79 in all other South African *Zosterops*).

From Portuguese East Africa also both yellows and greens have been reported by Dr. A. A. Pinto (1953) and through his kindness I have been able to examine good series, supplemented by ecological data supplied by him. The only typical green ones are from three localities:

(*a*) Namaacha, on the northern extension of the Lebombo Range, at about

2,300 ft., where patches of evergreen forest occur—conditions exactly like those in which green birds occur in Zululand.

(*b*) Umbelluzi, a locality practically at sea-level and devoid of evergreen forest, south-west of Lourenço Marquez. Yellow birds have also been collected here and greens would certainly not have been expected. The two greens (in the Smithsonian) were collected in July, and it has been suggested that they may be only winter-visitors to this untypical locality (Dr. Pinto, *in litt.*; Mr. D. W. Lamm, *in litt.*).

(*c*) Espungabera, *ca.* 2,800 ft. with evergreen forest patches, 400 miles to the north and only a few miles from Chirinda, over the border of Southern Rhodesia (see Map 8), has produced a typical yellow bird (wing 59, tail/wing ratio barely 70) and a typical green bird (wing 60, tail/wing ratio 75). As already noted, all the birds from the Rhodesian side of the border are all short-tailed and "yellow" except the one from Chimanimani that resembles the birds of the Nyasaland hill-forests. The Espungabera dark bird seems to be an isolated example of South African *virens*.

Thus, on the evidence from Zululand, the yellow and the green birds would certainly be regarded as specifically different. The Portuguese East African distribution is not so definitely in favour of this view, and moreover there are specimens whose plumage is intermediate. A male "yellow" from Umbelluzi (where, as noted, typical greens also occur) is darker and duller than the other Portuguese East African yellows; two females from Boane and Lourenço Marquez are darker above than the other yellows, and one of them also has as much melanin below as a green-belly. Interbreeding has, however, not been observed.

Taxonomic conclusions

These are reached with hesitation and must be regarded as provisional:

(*a*) Grey-bellies, *capensis* in the west intergrading with *atmorii* further east, are conspecific with green-bellies (*virens*).

(*b*) This group is specifically distinct from yellow-bellies (*anderssoni*).

(*c*) Pale-bellies (*pallida*) form a monotypic species. (There is no reason at all to connect them with other forms elsewhere in Africa that lack yellow on the belly.)

(*d*) Vaals ("*vaalensis*") are merely a colour-phase of *pallida*.

PART 5

INSULAR POPULATIONS

THE GULF OF GUINEA ISLANDS

The developments that have taken place in the Zosteropidae of the Gulf of Guinea are of special interest. Some of the birds concerned have so far differentiated that they have usually been regarded as worthy of separate specific and generic rank; and, unlike what happens on the African continent generally, apparently complete sympatry of two forms of Zosteropidae occurs in several cases. The situation is sketched diagrammatically in Text-fig. 11 with mean wing and tail measurements.

There are four islands, all of volcanic origin and lying on an axis S.S.W.–N.N.E. that extends to Cameroon Mt. on the mainland. Annobon appears to be drier than the other (very wet) islands, but all still carry a good deal of primary forest. Their age is uncertain, but they are believed to be post-Miocene, the result of the tectonic activity that has affected the whole of Africa since the end of the long early-Tertiary

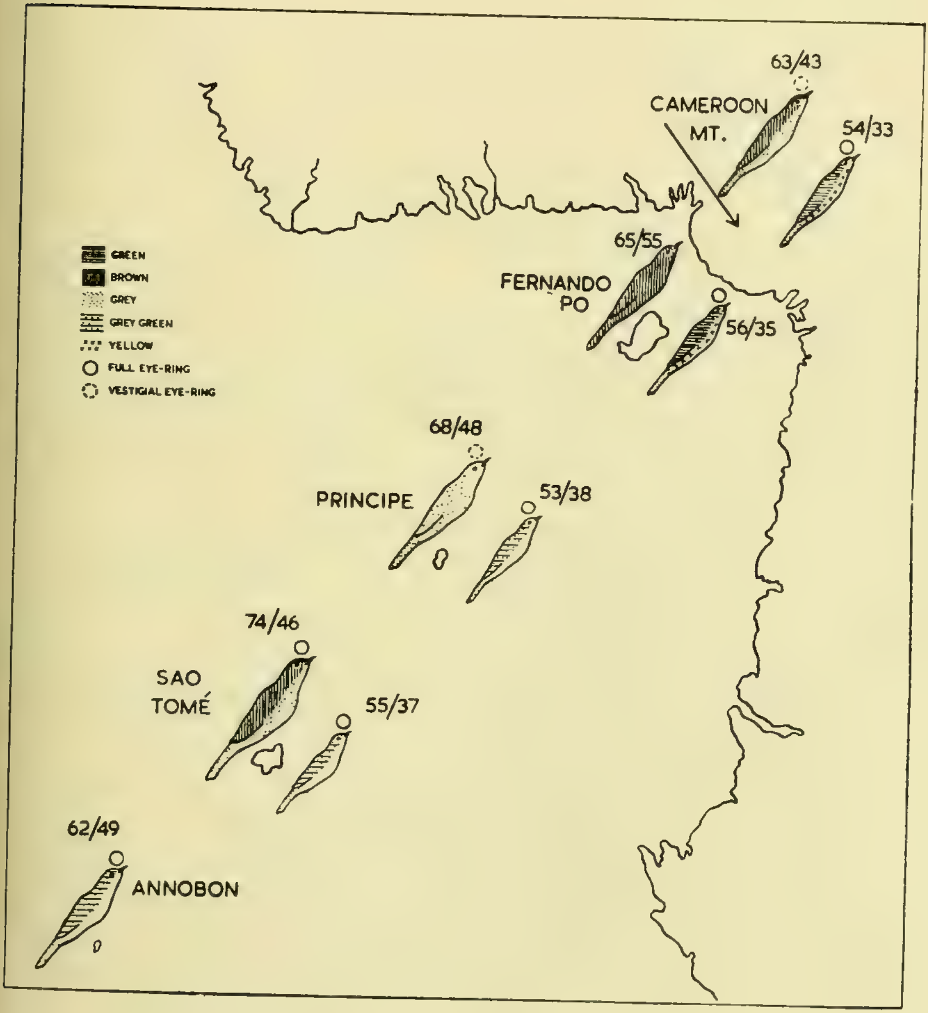

GREEN
BROWN
GREY
GREY GREEN
YELLOW
FULL EYE-RING
VESTIGIAL EYE-RING
63/43
CAMEROON MT.
54/33
65/55
FERNANDO PO
56/35
68/48
PRINCIPE
53/38
74/46
SAO TOMÉ
55/37
62/49
ANNOBON

FIG. 11. The Zosteropidae of the Gulf of Guinea.

calm. Exell (1944) has given a useful general account of the islands and Snow (1950) of the central pair, São Tomé and Principe, with particular reference to bird-habitats. Amadon (1953) has recently published lists, with a comprehensive discussion, of the Gulf of Guinea avifauna, in which, however, he has kindly left the Zosteropidae to me.

The islands (Text-fig. 9) are, from north to south :

Fernando Po, about 800 sq. miles, only 20 miles off-shore and rising to 9,300 ft. —133 species of birds.

Principe, 50 sq. miles, about 130 miles from Fernando Po and also from the mainland, and rising to 3,100 ft.—30 species of birds.

São Tomé, 400 sq. miles, about 85 miles from Principe, 140 miles from the mainland, and rising to 6,600 ft.—47 species of birds.

Annobon, under 7 sq. miles, about 110 miles from São Tomé, 210 miles from the mainland, and rising to 2,000 ft.—9 species of birds.

The three southern islands are typically "oceanic" in the biological sense and each is surrounded by water 6,000 ft. deep. Fernando Po is "continental", with sea only 200 ft. deep separating it from the mainland. There, little more than twenty miles from Fernando Po, stands Cameroon Mt., an isolated volcano rising to 13,300 ft., with which Fernando Po has the closest biological affinities. Indeed, for the purposes of the present discussion, Cameroon Mt. must be regarded as a Gulf of Guinea island. (The only other typically montane forest avifaunas in the western half of Africa are those on the mountains immediately to the north-east, Kupe, Manenguba and the Banso-Bamenda highlands, with which that of Cameroon Mt. has much in common.)

The diversity of the avifauna on each island is no doubt partly a reflection of its size and variety of habitats, but also partly of its chances of receiving immigrants. Throughout the year the wind over this eastern part of the Gulf of Guinea is predominantly S.S.W. (Meteorological Office, *in litt.*), thus favouring movement neither southwards down the chain Fernando Po–Principe–São Tomé–Annobon, nor direct from the continent to any of the islands. On biological grounds, from a consideration of the insular avifaunas as a whole, Amadon (1953) has concluded that each of the three oceanic islands must to a large extent have received its birds independently from the mainland.

Annobon is inhabited by only one member of the Zosteropidae, but Fernando Po, Principe, São Tomé and Cameroon Mt. are each inhabited by two, one larger and with less yellow pigment than the other. Dimensions are given in Appendix 3 (Part 2) and other salient details are summarized in Table 3 (see also Note 27, Appendix 3). Even though they show no striking modifications in beaks, there is, of course, a presumption that such sympatric pairs of closely related birds differ in their feeding habits, if not in their habitats (*cf.* Lack, 1944 ; Moreau, 1948). The larger birds of each of these Gulf of Guinea pairs differ widely between themselves, but they are all so different from normal *Zosterops* that they have been kept together in the genus *Speirops* (see Note 28, Appendix 1). It may be added that at least three

TABLE 3.—*Colour Characters of Gulf of Guinea Birds.*

	Colour of—					
Form.	Head.	Rest of upper parts.	Underparts.	Legs.[1]	Beak.[1]	Nature of eye-ring.
Aberrant:						
(1) Cameroon Mt. (*melanocephala*)	Blackish	Brown	Grey	Fleshy white or creamy white	Fleshy white or creamy white	Vestigial
(2) Fernando Po (*brunnea*)	Brown	,,	Brown	Dusky	Dark	Absent
(3) Principe (*leucophoea*)	Whitish	Grey	Pale grey	Pearl grey with yellow soles	Upper mandible dark grey, lower whitish	Vestigial
(4) São Tomé (*lugubris*)	Black	Olive-brown	Grey washed olive	Flesh	Yellow brown, upper mandible darker	Normal (medium)
Others:						
(5) Cameroon Mt. (*stenocricota*)	Yellow-green	As head	Yellow, flanks green	Grey	Black	Normal (medium)
(6) Fernando Po (*stenocricota*)	As (5)	,,	As (5)	,,	,,	,,
(7) Principe (*ficedulina*)	Olive-grey-green	,,	Whitish tinged sulphur	Pale brownish grey	Upper mandible dark horn, lower pale	,,
(8) São Tomé (*feae*)	Greyer than (7)	,,	Slightly greyer than (7)	Perhaps paler than (7)	Whitish tipped blackish	,,
(9) Annobon (*griseovirescens*)	Near (7)	,,	Near (7), fawn on flanks	Grey	Bluish horn	,,

[1] All except (1), (3), (4), (5) and (9) have, in the absence of collector's data, been based on colours of dried specimens.

of the *Speirops* and one of the insular *Zosterops* (São Tomé) differ from all the continental *Zosterops* examined by Dr. Auber in that melanization is not confined to the barbules but extends also to the barbs.

What little is known of the ecology of the nine birds may be outlined as follows :

(1) Cameroon Mt. at 6,000–9,000 ft. is inhabited by the brown endemic *Speirops melanocephala*, a bird which frequents the trees and shrubs in the montane grassland as well as clearings in the forest (Serle, 1950). Towards its lower limit this bird overlaps and associates with the smaller, yellow-green, *Zosterops stenocricota*, already discussed in Part 4.

(2) On Fernando Po, the common Zosteropid is the Cameroon *stenocricota* (see Note 27, Appendix 1) ; the other species, the endemic *brunnea*, is so rare that only two specimens exist in museums and nothing is known of its ecology.

(3) On Principe, the aberrant (grey) Zosteropid, *Speirops leucophoea*, is far bigger than its companion, the greenish *ficedulina*, but not bigger-beaked in the same proportion. No details are known of either bird, except that Snow (1950) found *leucophoea* in the lowlands, probably less abundant than it was first described to be in 1865, but yet more so than *ficedulina*, which he failed to see at all. (Correia collected some, however, in 1928—Amadon, 1953.)

(4) On São Tomé, the situation is like that on Principe. The aberrant bird, *Speirops lugubris*, is the largest of all the western Zosteropidae. Its disparity in wing-length with the *Zosterops* of the island, *feae*, is greater than that between any other of the pairs under discussion ; but, as in Principe, the two Zosteropids show rather less disparity in beak- than in wing-length. Snow (1950) found *lugubris* only from about 3,000 ft., above which it was common in the forest ; but he tells me that, unlike what obtains on Principe, such vegetation is lacking at the lower levels, so that *lugubris* may not be typically montane. Snow did not see *feae*, though Correia was able to collect a series in 1928 (Amadon, 1953).

(5) Annobon, so much smaller and less mountainous than the other islands, possesses only two passerines, a Paradise Flycatcher and the grey-green *Z. griseovirescens* (see Note 29, Appendix 1). It is the largest of the Gulf of Guinea *Zosterops*, smaller than the *Speirops*, but as big as most of the East African montane *Zosterops*. It was still plentiful throughout its wooded island when last reported in 1912 (by Boyd Alexander, in Bannerman, 1915).

When the foregoing information is considered together with the dimensions in Part 2 of Appendix 3, and the other characters outlined in Table 3, several points of interest emerge, which are discussed below.

Colour and pigments

All the insular Zosteropids have tended to lose yellow pigment with the exception of the Fernando Po *Zosterops*. This shows at most only incipient divergence from the nearby Cameroon *Zosterops*, presumably because of its recent arrival on the island or to frequent interchange of populations (or to a combination of these two factors).

As regards melanization, it is surprising that mainly (A)-type, i.e. black, pigment is present in the *Speirops*, which are predominantly brown or grey, and also in the São Tomé *Zosterops*, which is dull olive-grey-green. This colour is reproduced in the Principe *Zosterops*, which has not been examined microscopically, and also in the Annobon bird, but here its basis is (B) melanization (brown pigment). Since Annobon is much the driest island, the difference in pigment type is correlated with climate in the expected way. On the other hand, it is entirely unexpected that the colour (as distinct from the pigment) of the *Zosterops* should be so similar on both the wet islands and the dry, and also so like the colour of the dry-lowland *Zosterops* of Abyssinia. It appears that the pale colour of the São Tomé and Principe *Zosterops* cannot be a climatic adaptation.

Colour of beak and legs also tends to be abnormal in the Gulf of Guinea birds. On the African continent all beaks are black except some of the Abyssinian, which are brown. All the Gulf of Guinea birds depart from this in various ways. And in having their legs and feet whitish or flesh-coloured instead of more or less grey the Cameroon and São Tomé *Speirops* are distinguished from all the other Zosteropidae here reviewed.

The white eye-ring that occurs complete, though in a variety of sizes, in every *Zosterops* on the African continent, is vestigial in the black-headed *Speirops* of Cameroon Mt. and the white-headed *Speirops* of Principe and is completely absent in the brown *Speirops* of Fernando Po. Apparently the eye-ring is lost fairly easily in Zosteropidae, as has occurred in *uropygialis* of one of the Kei Islands, alone among the *chloris* group inhabiting that area (Stresemann, 1931). In the Gulf of Guinea the white eye-ring is being lost not only in a white-headed bird, in which contrast is in any case minimized, but also in a black-headed bird, in which contrast would be particularly strong.

Dimensions

In size—as judged by wing-length—the insular forms that are aberrant in plumage have also all become abnormally large. The Principe and São Tomé birds are both larger than any on the mainland of Africa. The only parallel is to be found in the most aberrant of the Pacific island birds, especially *Rukia*. Judging from the altitude/wing-length correlations on the continent (Text-fig. 1), the little-known Fernando Po bird is also abnormally large unless it is confined to the highest part of the 9,000-foot peak. Each of these aberrant birds presumably belongs to stock that has been longer on the island concerned than the less aberrant local *Zosterops*; and Amadon (1953) has already noted that the tendency of Gulf of Guinea insular birds to be big is especially marked in presumptive first-colonists such as these *Speirops* are.

From south to north the four *Speirops* form a series of diminishing size—São Tomé 74 mm., Principe 68, Fernando Po 65, Cameroon Mt. 63. No general reason can be suggested for this. As shown in Part 3, on the continent wing-length is closely correlated with both altitude and temperature. Lack of meteorological records and ignorance of the average altitude of the available specimens of each Gulf of Guinea form make it impossible to test the temperature correlation for these birds. It is, however, most unlikely that it would hold good, because the Cameroon *Speirops*, which is the smallest of the birds in question, comes from much the highest average altitude (8,000 ft.). The other stations are both more maritime and nearer the equator ; and there is no reason to suppose that the insular Zosteropids in question experience lower temperatures than the high-altitude birds of Cameroon Mt. I conclude that the large sizes attained by the *Speirops* are due to local biological causes and that there is no general reason for their arrangement in a series of decreasing wing-length northwards.

In contrast to the *Speirops*, except on Annobon none of the *Zosterops* diverges obviously in size from expectation (though again the data do not suffice for correlating wing-length with temperature). On Annobon, which does not rise above 2,000 ft., and which contains only one passerine besides the *Zosterops*, the latter is larger than expected. But on each "island" possessing two Zosteropids the less aberrant bird is the smaller, to a very variable degree. The difference in mean wing-length between *Speirops* and *Zosterops* is 19 mm. on São Tomé, 16 on Principe and only 9 mm. on Cameroon Mt. and Fernando Po.

Tail/wing ratios vary remarkably. At one extreme the Fernando Po *Speirops* appears to have a longer tail in proportion to wing (ratio over 82) than any other population of the western Zosteropidae (though individual South African birds exceed 80). At the other extreme the São Tomé *Speirops* has an abnormally short tail (ratio 61·8), equalled in this respect only by the *Zosterops* of the opposite mainland (as exemplified by those of Cameroon, with ratio 61·6). The insular *Zosterops* show a similar lack of uniformity. The Fernando Po bird is, like the Cameroon, abnormally short-tailed (62·8) by continental standards. The Principe and São Tomé birds have much higher, more "normal", ratios, 71·7 and 67·2 respectively, while the Annobon bird with ratio 77·6 is at the top end of the continental range. Thus there is no reason to regard the short tail of the São Tomé *Speirops* as evidence of particularly close affinity with the short-tailed but otherwise normal *Zosterops* of the neighbouring mainland. In fact, as discussed in Part 3, tail/wing ratio is of uncertain taxonomic significance.

The beak/wing ratio varies in the nine forms under discussion between 21% and 26%. The insular *Zosterops* have longer beaks in proportion to their wings than the insular *Speirops* (this does not apply to the Cameroon Mt. populations). In fact, against a mean beak/wing ratio of 22·7 for the continent of Africa as a whole, the mean beak/wing ratio of the *Speirops* in the Gulf of Guinea islands is only 21·3, while that of *Zosterops* is 24·5. Thus the *Zosterops*, but not the *Speirops*, accord with Amadon's (1953) generalization (based on other species) that insular birds tend to have larger beaks than their nearest relatives on the mainland. This might suggest that the *Speirops*, in the course of their evolution to their present stage of abnormality, passed through a phase in which their beak/wing ratio rose above that of the continental birds but that later, with increasing body-size, the process was reversed. On this hypothesis the Annobon bird is in the intermediate stage, with beak/wing ratio still high but body-size becoming abnormally large.

General

The Zosteropids of the Gulf of Guinea must have been derived originally from the opposite mainland, in at least some of the islands by two distinct colonizations. But which of the existing forms were evolved *in situ* from colonists direct from the mainland and which were derived from inter-island invasion cannot be determined. Any discussion could be little more than speculative, especially as the characters of the ancestral mainland *Zosterops* can only be surmised.

A main general change in all the insular birds is the loss of yellow pigment ; and it is difficult to suggest why this should be so, especially since, as has been shown, plumage colour is not correlated with climate.

The several *Speirops* differ from each other and from "normal" *Zosterops* in so many characters and to such varying degrees that it is impossible to decide which is the most primitive or the most "specialized". Those of Cameroon Mt. and São Tomé are sufficiently alike to be regarded as conspecific, and this although two islands, each with a very different *Speirops*, intervene geographically. The São Tomé bird has not lost eye-ring and yellow pigment to the same extent as the Cameroon bird, which suggests that the former is the nearer to the ancestral stock, and hence that the Cameroon bird is an invader from an island. On the other hand, the whitish on the forehead and throat of the Cameroon bird, which is lacking in the São Tomé, is adumbrated in those numerous "normal" *Zosterops* which have yellow on the forehead and throat contrasting with a generally green head. Hence in head-pattern the Cameroon bird may be regarded as retaining primitive characters that the São Tomé bird has lost. In any case it seems best to recognize the closeness of resemblance between the Cameroon and the São Tomé *Speirops* by treating them as conspecific. The Principe *Speirops*, with its very pallid foreparts, and the Fernando Po bird have evolved on different lines from the other two.

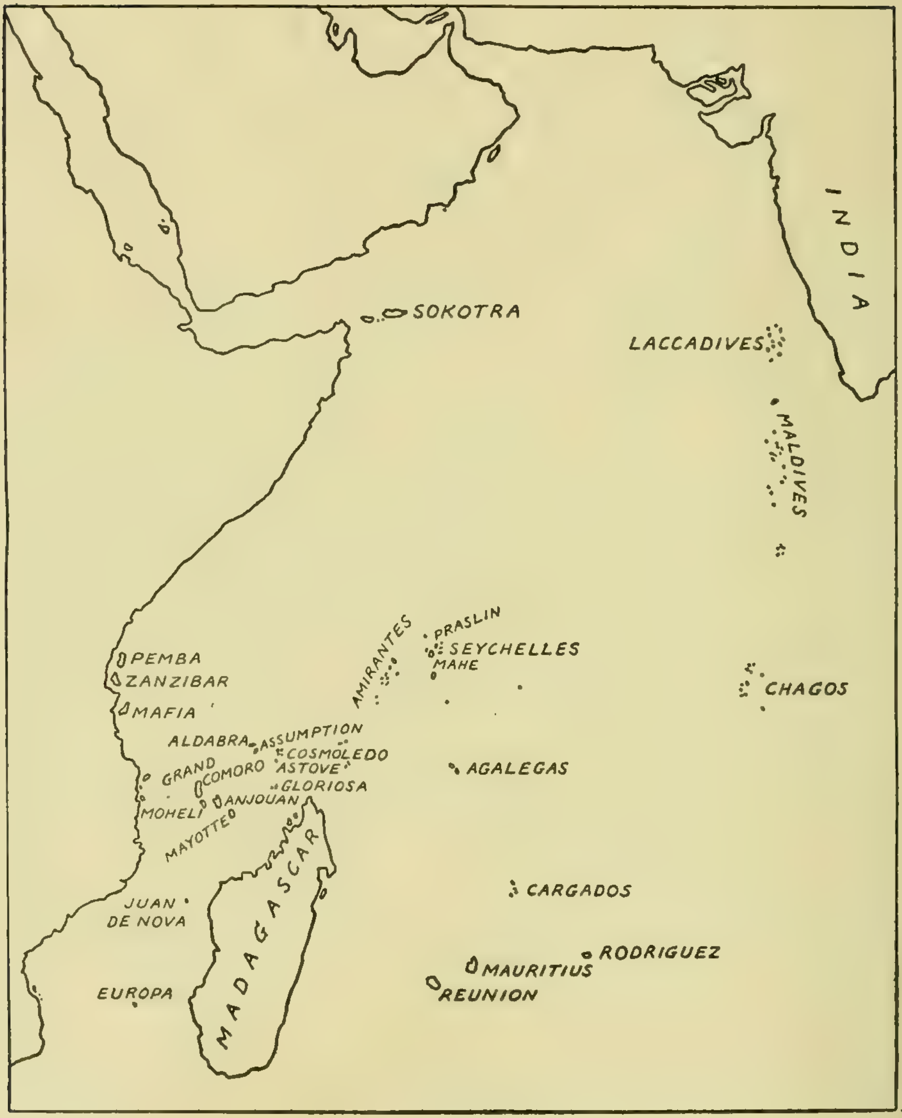
The *Zosterops* of Principe and São Tomé are so alike that one is more likely to have been derived from the other rather than both evolved, convergently, from independent colonists from the mainland. In general colour the Annobon *Zosterops* is so like these two that it has sometimes been regarded as conspecific ; but it is sufficiently different in size and proportions for this to seem undesirable.

Hence we get the following classification : *Zosterops senegalensis stenocricota* on Fernando Po, *Z. ficedulina ficedulina* on Principe, *Z. ficedulina feae* on São Tomé, *Z. griseovirescens* on Annobon. *Speirops lugubris melanocephala* on Cameroon Mt., *S. lugubris lugubris* on São Tomé, *S. brunnea* on Fernando Po and *S. leucophoea* on Principe.

THE ISLANDS OF THE INDIAN OCEAN

Zosterops are widely distributed in the Indian Ocean and belong to at least six species. Most of the islands fall into two groups (see Map 12), those inhabited by *Zosterops* being denoted in the following paragraphs by an asterisk.

(*a*) Low limestone islands, mostly atolls, of which there are a great many, especially in the east, where the Laccadive*, Maldive and Chagos archipelagos are separated


SOKOTRA
INDIA
LACCADIVES
MALDIVES
PRASLIN
SEYCHELLES
MAHE
AMIRANTES
CHAGOS
PEMBA
ZANZIBAR
MAFIA
ALDABRA
ASSUMPTION
COSMOLEDO
GRAND COMORO
ASTOVE
GLORIOSA
AGALEGAS
MOHELI
ANJOUAN
MAYOTTE
MADAGASCAR
CARGADOS
JUAN DE NOVA
RODRIGUEZ
MAURITIUS
REUNION
EUROPA

MAP 12. The Indian Ocean.

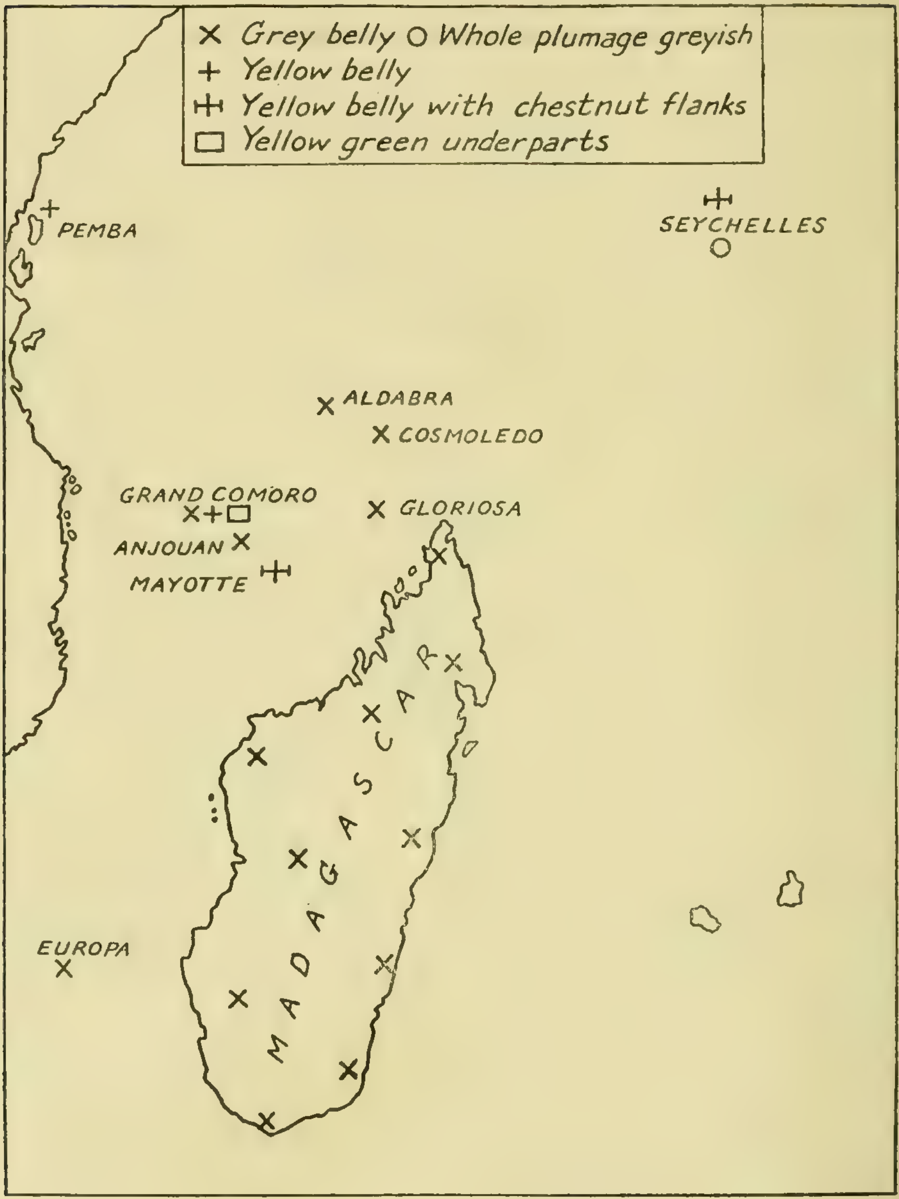
by 1,200 miles of uninterrupted sea from the Mascarenes. Other coral islands form the Cargados, the Amirantes, other outliers of the Seychelles and, nearer Madagascar, the Aldabra group*, Gloriosa*, and, in the Mozambique Channel, Juan de Nova (17° 4′ S., 47° 43′ E.) and Europa Island* 22° 20′ S., 40° 20′ E.). None of this class of island has an area of more than a very few square miles and most of them are only a few hundred acres. The natural vegetation appears to have been scrub jungle and much of it has been replaced by coconuts.

TABLE 4.—*Main Colour Characters of Indian Ocean* Zosterops.

N.B.—All have a small eye-ring.

Islands.	Upper parts.	Yellow on head.	Underparts.
Madagascar group :			
(1) Madagascar[1] *maderaspatana*	Yellow-green[1]	None.	Whitish more or less washed brownish grey
(2) Gloriosa	As the yellowest of (1)	,,	As (1)
(3) Cosmoledo	? Paler and less yellow than (1)	,,	,,
(4) Europa	As (1)	,,	,,
(5) Aldabra *aldabrensis*	Yellower than (2)	Variable on lores and forehead	,,
(6) Laccadives	Yellower than any above	As (5)	As (1) but clearer
Comoros :			
(8) Grand Comoro *comorensis*	As (2)	On lores and forehead	As (1)
(7) Anjouan *anjouanensis*	Slightly yellower than (1)	On lores	,,
(9) Grand Comoro *kirki*	Yellow green	On lores and forehead	Golden-yellow, green on flanks
(10) Grand Comoro *mouroniensis*	Greener than (9)	On lores	Greenish yellow
(11) Mayotte *mayottensis*	Greenish-yellow	On lores and forehead	Golden yellow, reddish at sides
Seychelles :			
(12) Marianne *semiflava*	Slightly yellower than (11)	Less than (11)	Brighter than (11)
(13) Mahé *modesta*	Grey-brown tinged olive	None	Pale grey-brown
Mascarenes :			
See Table 5			

[1] Marked local variation, the birds being darkest in the wettest areas, yellowest in the driest.


× Grey belly ○ Whole plumage greyish
+ Yellow belly
ꟷ+ꟷ Yellow belly with chestnut flanks
☐ Yellow green underparts
PEMBA
SEYCHELLES
ALDABRA
COSMOLEDO
GRAND COMORO
GLORIOSA
ANJOUAN
MAYOTTE
MADAGASCAR
EUROPA

MAP 13. The distribution of *Zosterops* colour in the Indian Ocean islands.

(*b*) Other "oceanic" islands, the Comoros*, Mauritius*, Reunion*, Rodriguez and the Seychelles*; most of these are mountainous and all are volcanic except the last. They range in size from the single square mile of (granitic) Marianne in the Seychelles to the 270 square miles of Mauritius. All seem to have been covered with forest when discovered about 400 years ago, the smallest of the Seychelles being the driest. The Seychelles group, the Comoros group and each of the other islands are surrounded by deep water. Nothing certain is known of their age, but in view of the general tectonic tranquillity during the earlier half of the Tertiary there is little doubt that the volcanic islands are post-Miocene; the Seychelles may well be much older.

Apart from these two classes of typically oceanic islands there are in our area :

(1) the great island of Madagascar*, which is in a class by itself ;

(2) numerous islets which are no more than the tips of coastal reefs surrounding Madagascar or the African continent ;

(3) the two big inshore islands of Zanzibar and Mafia (640 and 240 square miles), typically "continental" both biologically and geographically ;

(4) Pemba Island* (380 square miles), less than thirty miles from the African mainland but not typically continental.

(5) Sokotra* (and neighbouring islands) off the "Horn of Africa" (Somaliland). Its *Zosterops*, which is like the Somali bird, has already been dealt with in the section "North-east Africa".

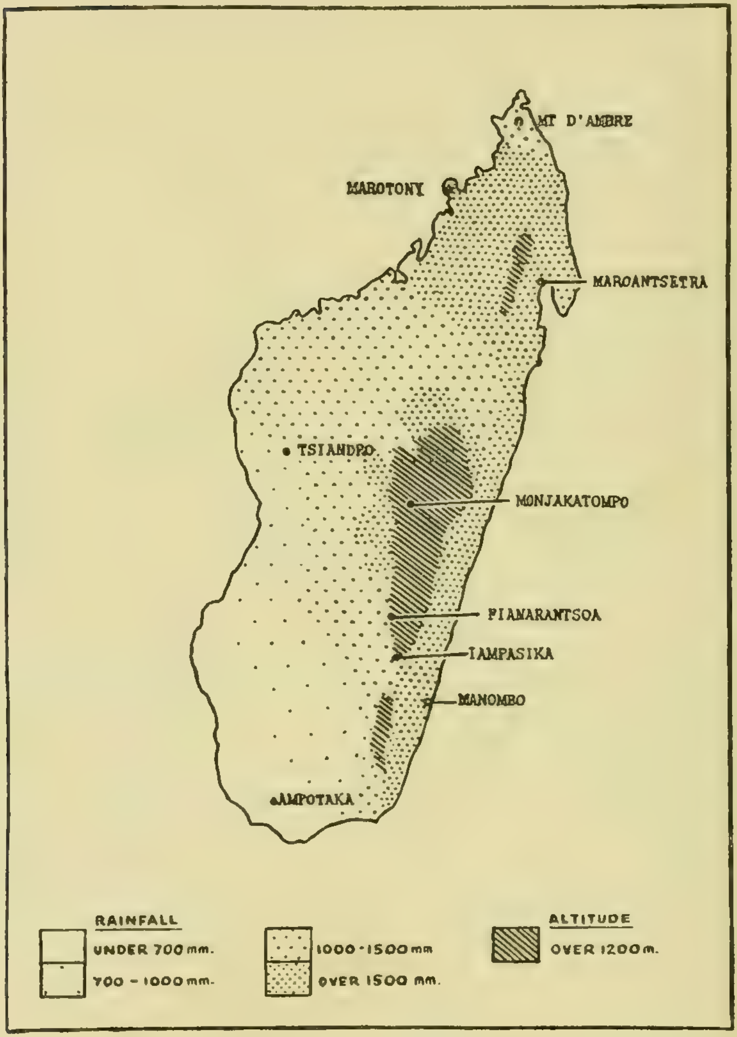
The main colour-characters of the Indian Ocean *Zosterops* are outlined in Table 4 (dimensions in Appendix 3, Part 3) and the distribution of these is given in Map 13). The island populations will now be dealt with separately.

Pemba Island

Pemba is geologically and biologically peculiar (Moreau and Pakenham, 1941). Though only thirty miles from the African coast it is separated by water 2,000 ft. deep and has a *Zosterops* as one of its commonest birds (Vaughan, 1930) ; whereas the neighbouring islands of Zanzibar and Mafia, which are on the continental shelf, lack *Zosterops* though apparently suitable for them. The Pemba bird, *vaughani*, is small and richly coloured, with an unusually bright golden-yellow forehead. In this respect (though no other) it approaches the montane *Zosterops* of eastern Kenya, but it is separated geographically from these by other *Zosterops* that are very different. There is also no reason to suppose that the *Zosterops* now occupying the nearby East African lowlands (*flavilateralis*), which looks very different from the Pemba bird, was its ancestor or is particularly closely allied ; and there seems no alternative but to treat the Pemba bird as a monotypic species.

Madagascar

As shown in Map 14, the driest parts of Madagascar (200,000 sq. miles) are the extreme northern tip, with rainfall under 40 inches, and the south-west, with under 30 and a strongly xerophytic vegetation. The whole of the east coast, except the far north, is wet (rainfall 60–140 inches) with much of the natural vegetation evergreen


MT D'AMBRE
MAROTONY
MAROANTSETRA
TSIANDRO
MONJAKATOMPO
FIANARANTSOA
IAMPASIKA
MANOMBO
AMPOTAKA
RAINFALL
UNDER 700 mm.
700 - 1000 mm.
1000 - 1500 mm
OVER 1500 mm.
ALTITUDE
OVER 1200 m.

MAP 14. Madagascar.

forest ; and rainfall of over 60 inches extends across to the north-west coast. Most of Madagascar is lowland, but the land rises to 8,600 ft. in the east centre, and further to the north and south there are small detached areas above 4,000 ft.

Because so much of the Madagascar fauna is highly peculiar it is surprising that the single species of *Zosterops* occurring there should be "normal" and unspecialized. With its green upper parts and whitish underparts more or less clouded with grey the Madagascar *Zosterops* resemble many others, notably those of Abyssinia. In different parts of the island they vary in size and in the amount of melanin. The darkest birds are found in the area of highest rainfall in the east ; those with yellowest backs (least melanin) come from the extreme south-west, and the next yellowest from Mt. d'Ambre, in the dry area at the opposite end of the island. Intervening birds (for example, a series from Tsiandro) are intermediate in colour, while birds from the north-west, round Marotony, cannot be distinguished from those with the same rainfall, about 1,500 mm., in the south-east (Manombo). As regards the underparts (in which the individual variation is great), birds from the wettest area in the island, Maroantsetra on the north-east coast, have on the whole the most (and more brownish) grey shading than any others, and those of the dry south-west have the least.

Size also varies as expected, in that birds from the highest locality (in the east centre) are the biggest. However, the smallest are from two detached areas, the very wet Maroantsetra on the north-east coast, and the south, including both Ampotaka, which is very dry, and Manombo, which is rather wet. Comformably, the south-western birds have slightly the smallest beaks, as Salomonsen (1934*b*) has claimed.

Salomonsen (1934a, 1934b) described the yellowest, "dry", birds as *ampotakae* and the biggest birds as *analoga*, confining *maderaspatana* to the humid east at low altitudes and considering that many birds in the island are intermediate between *ampotakae* and *maderaspatana*. Rand (1936), on the other hand, while recognizing that the birds from the south-west and from the extreme north are both yellower than those in between, is content to call all the western birds *ampotakae*—with the extraordinarily wide habitat-range of "humid forest, dry forest, secondary brush and subdesert brush". As regards the large "subspecies" *analoga*, there is no doubt that the virtual discontinuity claimed between its size-range and that of *maderaspatana* is due to paucity of samples from intermediate altitudes (see Note 30, Appendix 1). In fact the true picture of the Madagascar *Zosterops* is of a series of trends in size and intensity of melanin that are in conformity with the changing environment. The use of three trinomials tends to obscure the biological facts. (For the individuals lacking carotenoid, on which *Z. hovarum* and *Z. praetermissa* were described, see Note 2, Appendix 1.)

The Comoro Islands

The Comoro group consists of four volcanic islands (with very few off-lying islets), the most westerly, Grand Comoro, being 180 miles from the African mainland and the most easterly, Mayotte, 190 miles from Madagascar. Each island is in sight of one or two others, 30–60 miles distant. Approximate sizes and altitudes are :—

Grand Comoro, 420 sq. miles, 8,000 ft. ; Mohéli (Mohilla), 150 sq. miles, 2,400 ft. ; Anjouan (Johanna), 140 sq. miles, 4,900 ft. ; Mayotte, 140 sq. miles, 2,000 ft.

Apparently a larger proportion of the original forest is left on them than on the other islands in the Indian Ocean (Grandidier, 1934). Individual islands have from one to three different *Zosterops* on them, as follows :

(1) The Mayotte *Zosterops* is short-tailed (ratio 63) and bright yellow with chestnut on the flanks (sometimes extending across the breast). It is unlike every other *Zosterops* except *semiflava* of the Seychelles, 800 miles away to the north-east, and particularly unlike the neighbouring Madagascar birds. Nothing is known of its ecology except that Nicoll (1908) found it one of the commonest birds of the island, "especially on the edges of the mangrove swamps".

(2) Anjouan birds differ from those of Madagascar only in being a little yellower, with a tendency for the yellow on the throat to extend a little further down the breast. Anjouan beaks are also perhaps a trifle stouter than those on Madagascar or Aldabra (Friedmann, *in litt.*, agrees), but in other dimensions there is little difference from Madagascar birds. Nothing has been recorded of the Anjouan *Zosterops* in life. It is apparently confined to that island, the record of *anjuanensis* for Grand Comoro in Shelley (1879) and Milne-Edwards and Oustalet (1888) really relating to *comorensis* (see below).

(3) On Mohéli Völtzkow (1917) recorded *kirki*, one of the Grand Comoro birds (see below). This may or may not be correct. No museum seems to possess a Mohéli *Zosterops* and Professor Stresemann (*in litt.*) thinks Völtzkow's record is on sight—useless in such a case.

(4) Grand Comoro, the biggest and loftiest of the four islands, seems to have three *Zosterops*. Nothing is known of any of them in life.

(*a*) *Z. comorensis*, a bird with a whitish belly (see Note 31, Appendix 1) was described by Shelley from a single specimen, in poor condition and not sexed, which is still the only one known. It differs from the Madagascar and the Anjouan birds only in having a little more yellow on the front of the head and being a little smaller. In conjunction, these slight differences suggest that the specimen does represent an indigenous Grand Comoro population rather than being merely wrongly labelled or a straggler from Anjouan, sixty miles to the east. Only field-work can settle this.

(*b*) *Z. kirki* is a richly coloured yellow-bellied bird with a range of wing-length and tail-length that includes the dimensions of the only specimen of *comorensis*. Moreover the tail/wing ratio is the same and the beak practically so. The possibility that this and *comorensis* are merely colour-phases cannot be ruled out.

(*c*) The third *Zosterops* described from Grand Comoro, *mouroniensis* (see Note 32, Appendix 1), is quite distinct from any other of the Indian Ocean birds ; it is large and dark, and the only one to have yellow underparts heavily flushed with green. Its wing averages 62 compared with 53 in the other *Zosterops* on the island, and its tail/wing index is the abnormally high one of 79, which compares with 67. The beak of *mouroniensis* is not, however, proportionately longer and stronger than it is in the smaller birds. This is correctly suggested in plate 5 of Milne-Edwards and Oustalet (1888), though the plumage is probably there depicted too yellow. The large size and dark plumage of *mouroniensis* are exactly what would be expected in a highland bird, but it is not known to be so, although the island contains a 9,000-foot mountain.

The Seychelles

This mountainous group is more isolated than the Comoros, being 900 miles from the African mainland (with no islands on the way), 600 from Madagascar (with atolls at intervals) and about 500 from Aldabra, the nearest *Zosterops* population. E. Newton (1867) found that at least five of the islands supported from two to five species of native passerines and Vesey-Fitzgerald (1940), while chronicling some disappearances, was able to record also some additions. It is therefore remarkable that the only certain evidence of Zosteropidae in the Seychelles is of one form (*modesta*) on Mahé (55 sq. miles, the biggest of the group) and one (*semiflava*) that formerly inhabited tiny Marianne Island, less than one square mile (see Note 33, Appendix 1).

In size, proportions, eye-ring and beak, both *modesta* and *semiflava* are typical *Zosterops* and are very much alike ; but their colourings are as different as possible (see plate 6 in Shelley 1900, vol. 2). *Z. modesta* is a muddy-brownish bird almost entirely devoid of yellow pigment. Vesey-Fitzgerald (1940) has already noted that most of the Seychelles passerines have tended towards the same dingy olive plumage, as elsewhere in small isolated avifaunas. By contrast, *Z. semiflava* has bright olive-yellow upper parts and golden yellow under-parts with bright chestnut sides. Thus *semiflava* is unlike any other *Zosterops* except the Mayotte bird 800 miles away to the south-west (and with the very different Madagascar type of *Zosterops* on intervening atolls). Indeed *mayottensis* differs from *semiflava* only in being smaller and slightly yellower.

From its loss of yellow it is probable that *modesta* is a descendant of a much earlier invader of the islands than *semiflava* is. Since these two are so alike in size and beaks (and probably in habits) it is unlikely that they could co-exist for long on such small individual islands and they may at one time have divided the archipelago between them.

The Mascarene Islands — Réunion (Bourbon) and Mauritius

Réunion lies nearly 500 miles east of Madagascar and Mauritius 120 miles further east, but under 600 miles from the nearest point of Madagascar. Each is a volcano, probably not older than the Pliocene (Réunion is not extinct) and is surrounded by very deep water. Mauritius, with an area of 720 square miles, rises to 2,600 ft., Réunion, about 1,000 square miles, to over 10,000 ft. Since there is no land to the east bigger than Rodriguez (42 sq. miles) for 2,000 miles, the chances that Mauritius and Réunion received their birds from Madagascar are overwhelming, but the present wind-system does not favour dispersal in this direction. All through the year easterly winds predominate on the east side of Madagascar and in Réunion (Grandidier, 1934). Moreover the tracks of the local cyclones, potentially even more important agents of dispersal, are nearly all unhelpful. Of 74 cyclones plotted in this area (west of 70° E.) 1927–1937, only two passed over the east coast of Madagascar and then within 100 miles of either Mauritius or Réunion (Huddart, 1948).

Considering their isolation, the parallelism between the avifaunas of the two islands is remarkable. Nearly all the passerine species are common to both islands, and in the Zosteropidae each island possesses a long-beaked one that has lost some of its yellow pigment, and a short-beaked one that has lost all its yellow and its white eye-ring as well (see Note 34, Appendix 1). The plumage features of all four birds are summarized in Table 5, dimensions in Appendix 3 (Part 3).

TABLE 5.—*Colour Characters of Réunion and Mauritius Zosteropidae.*

	Head.	White eye-ring.	Upper tail-coverts.	Colour of rest of upper parts.	Under parts
borbonica (Réunion)	Brown	Absent	White	Brown	Whitish with cinnamon flanks
mauritiana (Mauritius)	Grey	,,	,,	Grey	Whitish with grey-brown flanks
haesitata (Réunion)	Blackish	Marked	Yellow-green	Yellow-green	Grey, more rufous on flanks; under-tail coverts greenish yellow
curvirostris (Mauritius)	Dark grey	,,	,,	Grey, becoming green on lower back	As *haesitata*

Briefly, *borbonica* on Réunion is a small brownish bird of normal proportions (wing 55, tail/wing ratio 73) with a beak (*ca.* 13·5 mm.) if anything weaker and more pointed than in typical *Zosterops*. Individual variation in adult plumage is exceptionally high (grey to brown), while the immature plumage is more uniformly brown (Berlioz, 1946). The Mauritian representative of *borbonica*, *mauritiana*, also completely devoid of yellow pigment, is usually grey, sometimes brownish. The greyest birds from Réunion are little browner than the brownest from Mauritius ; and the two populations are alike in dimensions and in having white rumps. This last feature is presumably merely a derivative of the pale colour (yellow) on the rump which occurs in many *Zosterops* in Africa and elsewhere. There is no strong case for retaining these Mauritius and Réunion birds in a separate genus, *Malacirops*, nor for treating them as two separate species, as has been done in the past.

In both of the other pair of birds, *haesitata* of Réunion and *curvirostris* of Mauritius, the beak/wing ratios are higher than in any other western Zosteropidae and are exceeded only in a few forms on small islands in the Pacific. In both, yellow pigment has gone from the head, but the Réunion bird is more melanic than the Mauritian and also larger (wing 57·7 compared with under 52) and longer-tailed (ratio 70 against 63).

The present status of the Réunion birds has been described by Milon (1951). He found the smaller-beaked *borbonica* "très commun partout", with occupied nests from sea-level up as far as he went (1,300 m.). The longer-beaked *curvirostris* was "assez commun en fôret" from 500 m. upwards. This species is, then, more of a forest (and mountain) bird than the other. This is the reverse of what Pollen and Dam (1868) recorded over eighty years ago, but agrees with the distribution of the two related birds on Mauritius (see next paragraph). Milon also records that in the mountains they regularly inhabit the same biotope, trees and bushes. Their overlap leads him to postulate a difference in feeding habits (as the difference in beaks also strongly suggests), but he was unable to prove it. It is interesting that in Réunion *curvirostris* is regarded as having suffered much more severely than *borbonica* from the 1948 cyclone, a difference that might be connected with a tendency for the latter to roost nearer the ground (Milon, 1951).

On Mauritius the grey *mauritiana* has survived more generally and in larger numbers than the longer-beaked *curvirostris*, which is, as Meinertzhagen (1912) found, mostly in the remote forests of the south-western plateau and not numerous there (Dr. R. Vinson, *in litt.*, 1951). Apparently the two Mauritius species do not associate together (*ibid.*). *Z. curvirostris* is supposed to have suffered through destruction of its nest by the bulbul *Otocompsa jocosa*, which was introduced into Mauritius a hundred years ago, but not into Réunion (Berlioz, 1946). In Mauritius, as in Réunion, there are no observations on the food-habits of the two *Zosterops* which suggest specialization, though the difference in beaks suggests it.

The two birds devoid of yellow pigment, *borbonica* and *mauritiana*, differ only in that the Réunion bird is browner and has a beak a little narrower at the base than the Mauritius bird. By contrast, in the other, long-beaked, pair of birds, those of Mauritius are much smaller and shorter-tailed. Yet the beaks are nearly the same size, so that the beak/wing ratio in Mauritius is nearly 32 against 27 in Réunion. In Réunion the long-beaked *Zosterops* is a bigger bird than the short-beaked, but in Mauritius this is reversed. Yet the difference in each island between the beak-lengths of the two Zosteropids is the same, about 2 mm.

It is by no means clear whether *borbonica* and *mauritiana* or *haesitata* and *curvirostris* represent the earlier invasion into the Mascarene islands. The first pair have lost their eye-ring and all their yellow pigment and have acquired the unique feature of white upper tail-coverts. The second pair have lost the carotenoid from their throats, but not from all their upper parts, and they have considerably modified beaks. The beaks are in fact rather like those of *Zosterops zeylanica* (Ceylon), in which this change has taken place before pigment has been lost in the plumage. It seems that the present situation in the Mascarenes—both species present on both Réunion and Mauritius—could have arisen in two ways. Either *Zosterops* from Madagascar colonized Réunion or Mauritius ; later, when the first colonists had already diverged considerably from "normal" *Zosterops*, a second invasion succeeded in establishing itself on the same island and also proceeded to diverge from the normal ; then both at some later stage colonized the other island. Alternatively, and perhaps more likely, opportunities being what they were, Madagascar *Zosterops* colonized Mauritius and Réunion independently, the stock on each diverged from the "normal" and subsequently, when the evolution had gone far enough, each succeeded in establishing itself on the other's island.

Whichever of these hypotheses is correct, the fact that the Zosteropids, and most other passerines, on Mauritius differ at most subspecifically from those on Réunion, makes it most probable that interchange between them has not been infrequent ; the winds, as already noted, strongly favour movement from the outer island, Mauritius to Réunion, but not the other way.

The remaining islands

All the remaining insular populations are of Madagascar type, with whitish belly, and they occur on islets north and west of Madagascar except for those on the Laccadives, which are on the opposite side of the ocean, close to the Indian coast.

(1) On Aldabra, a dissected atoll about fifty miles round, the *Zosterops* is a little yellower, smaller and longer-tailed than Madagascar birds.

(2) On Gloriosa, less than two square miles, about 115 miles from the north end of Madagascar, the *Zosterops* are not distinguishable (see Note 35, Appendix 1). Nicoll (1906) found it "the most abundant land-bird" but there cannot have been more than a few hundreds.

(3) On Cosmoledo and Astove, fragmentary atolls between Aldabra, Gloriosa and Madagascar, *Zosterops* are common (Vesey-Fitzgerald, 1940) but material is insufficient to show whether the birds are distinctive (see Note 35, Appendix 1).

(4) On Europa, in the Mozambique Channel, sixteen square miles, about 250 miles from both Africa and Madagascar, the *Zosterops* differs from Madagascar birds only in having a higher tail/wing ratio (see Note 36, Appendix 1).

(5) The Laccadive *Zosterops*, while of the same colour-pattern as the preceding, is undoubtedly derived from the neighbouring Indian mainland. Ticehurst (1927) and Stresemann (1931) attributed them to the Ceylon subspecies *egregia* which would imply either invasion of the Laccadives from Ceylon round the tip of the Indian peninsula or convergent evolution. However, *egregia* is very like *occidentis* of western India and on comparing series I find that the Laccadives birds are actually intermediate in plumage.

General discussion

Considering the bigger sea-distances, the Indian Ocean Zosteropidae show less marked peculiarities then might have been expected from the situation in the Gulf of Guinea. The Indian Ocean birds as a whole tend to be slightly longer-beaked (mean ratio over 24) than would be expected by continental standards, but there is no gigantism, and where yellow pigment is lost the result is not the same dingy pallor of plumage as in the Gulf of Guinea *Zosterops*. On the Indian Ocean atolls the *Zosterops* have differentiated particularly little, even though the populations are so small, and they must all be regarded as correspondingly recent invaders.

It is remarkable that the *Zosterops* of Madagascar, an island possessing so many outstanding endemics, should not be in the least specialized. On the contrary they are so like both the Indian birds (*palpebrosa*) and certain African birds that convenience is the main reason for keeping them as distinct species.[1] It is possible that *Zosterops* of modern type were already in occupation of Madagascar before it was isolated from Africa. The generally accepted view is that this took place late in the Miocene (some twenty million years ago), when many of the present African genera may already have been in existence (see discussion in Moreau, 1952). It is true that the African *Zosterops* most like those of Madagascar do not occur on the continent just opposite the island, but the present *Zosterops* picture on the mainland is perhaps very recent on the evolutionary time-scale.

The Madagascar *Zosterops* may have remained "normal", partly because the area is so large and the fauna so rich—not typically insular—and partly because the original stock, if merely cut off from the continent, not invading, would have had so large an assortment of genes that there was no intrinsic tendency to unbalanced differentiation in the isolated environment (*cf.* Mayr, 1954). In any case, unless the Madagascar stock that gave rise to the *Zosterops* of Réunion and Mauritius has been superseded by the existing one, this has remained stable while two eccentric developments have taken place in the smaller islands.

The *Zosterops* of Aldabra, Anjouan, Gloriosa, Europa and Cosmoledo, as well as *comorensis*, resemble those of Madagascar so closely that they are probably all (down-wind) colonists from there. If their appearance is a guide, the other two *Zosterops* of Grand Comoro are successive invaders from Africa. This would be in line with the conclusion, reached by Milne-Edwards and Oustalet (1888), that the (highly endemic) Comoro avifauna as a whole has been derived from both Africa and Madagascar. If indeed two *Zosterops* so alike as *kirki* and *comorensis* co-exist on Grand Comoro it can only be through genetical incompatibility, and that would be more likely if the birds were derived from western and eastern stocks respectively.

Nothing can be hazarded about the origin of the Mayotte and Seychelles *Zosterops*, which are all three peculiar. But, because they share the very rare colour-combination of bright yellow and reddish, *mayottensis* and *semiflava* must have had a recent common ancestor, even though other, Madagascar, types of *Zosterops* intervene geographically. The wide geographical separation of these subspecies and of those of the Réunion and Mauritius *Zosterops* finds a counterpart in Micronesia, where subspecies of *Z. conspicillata* and *Z. cinerea* are dispersed over much greater marine distances in the Caroline and Palau islands (Baker 1951).

The following taxonomic arrangement seems justifiable :

Z. maderaspatana maderaspatana (Madagascar, Gloriosa and perhaps Cosmoledo), *Z. m. aldabrensis*, *Z. m. völtzkowi*, *Z. m. comorensis* ; *Z. senegalensis kirki* ; *Z. mouroniensis* ; *Z. semiflava semiflava*, *Z. s. mayottensis* ; *Z. modesta* ; *Z. borbonica borbonica*, *Z. b. mauritiana* ; *Z. curvirostris curvirostris*, *Z. c. haesitata.*

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[1] For example, some birds from Madagascar match birds from Abyssinia (*poliogastra*) except in lacking yellow on the forehead and having the throat a stronger, less greenish, yellow. Again, Madagascar birds differ from the grey-bellied birds of the Cape only in the shade of green on the upper parts, purer yellow of the throat, and paler underparts, especially in the centre.

PART 6

SYNTHESIS

Throughout this study the overwhelming general impression has been the close correlation of the *Zosterops* dimensions with altitude and temperature, and also the correlation, though less constant, between colour of plumage and type of climate. These correlations on the one hand ensure high local variation, largely clinal, and on the other hand favour convergent evolution. The first of these results means that, if trinomial nomenclature is applied, the variation admitted within the subspecies must, for practical purposes, be wide and the delimitation of their range cannot be precise. The second result means that, following current ornithological usage, on purely morphological criteria the same subspecific name will on occasion be used for geographically remote populations that are convergent products of independent local evolution. So far as the problem of the specific limits of the African *Zosterops* is concerned the obvious guiding principle is that forms which intergrade geographically and in characters must be treated as members of the same species (*cf.* Cain, 1954) ; special difficulties arise where there are discontinuities, as between islands.

It will have been evident, particularly from the discussion on the significance of belly colour (Part 2), that attempts to use the colour aspect of "morphological" difference consistently as a specific criterion in *Zosterops* must break down. We are repeatedly thrown back on the criterion of occurrence of interbreeding, one particularly unsatisfactory in these *Zosterops*, where hybrids are likely to be difficult or impossible to diagnose with certainty and series of critically collected material are not as a rule available. As mentioned in the introduction, interbreeding between two "morphologically" different forms of *Zosterops* that are neighbours in Africa rarely seems quite impossible on grounds of "genetical allopatry" ; and a few specimens have been mentioned in the text that look as if they were hybrids. If such hybrids form only a small proportion of the total *Zosterops* population where two forms meet, or the zone in which hybrids occur is narrow, and/or the hybridization is of the "secondary" type, with high variation between the hybrid individuals, then the parents are best treated as belonging to different species.

When these principles are applied to the *Zosterops* described in this study the conclusions reached as regards the specific limits cut right across previous classifications, which have been on a purely "morphological" basis, in fact on colour. Now, though admittedly evidence of intergradation is not as complete as could be wished, the following are the logical deductions :

(1) The yellow *senegalensis* of West Africa is conspecific with the darker (more greenish) birds of Sierra Leone and Liberia (*demeryi*), of the wet area round the head of the Gulf of Guinea (*stenocricota*), and of southern Uganda (*stuhlmanni*).

(2) Darkening further, both eastwards and westwards, *stuhlmanni* is conspecific, via the Yala birds, with *jacksoni* of the western Kenya Highlands and

certainly intergrades with (*a*) the smaller birds (*toroensis*) of Bwamba–Ituri on the eastern edge of the Congo basin and (*b*) with the larger birds of Ruwenzori, Kivu and the mountains north-west of Lake Tanganyika (*reichenowi*), which are among the darkest and greenest in Africa.

(3) West and south through the southern Belgian Congo, *reichenowi* intergrades with the yellower *anderssoni*, of the southern tropical belt, some representatives of which are very like some from the north of the equator. Through central Angola the yellow *anderssoni* intergrades with the large dull *quanzae*, and this, north-eastwards through northern Angola and south-western Belgian Congo, with the smaller and yellower *kasaica*.

(4) The varied birds, some yellower and some greener (usually called *anderssoni* and *stierlingi*) of Nyasaland and south-western Tanganyika Territory (north to Uluguru and Usambara) form a special case. There is no proof of intergradation on any particular mountain in Nyasaland, but (*a*) different areas between them produce a complete series of intermediates, (*b*) local trends in colour can be traced through the highlands southwards from Iringa. Moreover on the Imatong group of mountains, isolated by many hundreds of miles from the *anderssoni-stierlingi* complex, there are indications of intergradation from yellow West African *senegalensis* to greener birds that are indistinguishable from Nyasaland *stierlingi*.

(5) The dull-coloured birds of the south-eastern Abyssinian lowlands and Italian Somaliland (*jubaensis*) intergrade southwards through Kenya and Tanganyika to the larger, more yellow-green, *flavilateralis*.

The relationship of (4) to (1)–(3) remains to be discussed, together with the other outstanding problems in north-eastern Africa, Kenya, Tanganyika and South Africa. Thus, on the basis of the foregoing, two distinct groups, each of intergrading forms, are established at the outset :

Z. senegalensis, including all the *Zosterops* from Senegal to western Abyssinia and south through western Kenya and central Africa to southern tropical Africa.

Z. jubaensis, southern Abyssinia to central Tanganyika.

The fact that belly-colour is not necessarily a specific criterion leads not only to the acceptance of the South African forms *capensis-atmorii* and *virens* as conspecific, which seems proved by the extensive interbreeding, but also to the following conclusions, for which such evidence is lacking :

(6) In the Abyssinian highlands, the yellow-bellied *kaffensis* is conspecific with the grey-bellied *poliogastra*.

(7) In the Abyssinian lowlands, the grey-bellied *abyssinica* and *omoensis* are conspecific with the yellow-bellied *jubaensis* (and hence with *flavilateralis*, extending south to central Tanganyika).

(8) In Kenya and Tanganyika the grey-bellied *kulalensis*, *silvana* and *winifredae* are conspecific with the yellow-bellies on the neighbouring mountains, *jacksoni*, *eurycricota* and *mbuluensis* respectively.

Because interbreeding between the following contiguous forms is at most rare, the following groups are regarded as specifically distinct from each other :

(9) South African *virens* from the *senegalensis* (*anderssoni*) group with which it interdigitates near Mozambique. This conclusion is reached in the face of the fact that in plumage some South African specimens are extremely like some from the Nyasaland mountains (allocated in (5) above to *senegalensis*), but is supported by the small but constant difference in tail/wing ratios.

(10) Highland Abyssinian birds, group (6) above, from lowland, group (7).

(11) Lowland *abyssinica-flavilateralis*, group (7), from the various populations which they surround on the mountains of Kenya and northern Tanganyika.

(12) (West African) *senegalensis* from the *abyssinica* forms, group (7), that it overlaps round Lake Tana.

(13) *Z. pallida*, of south-western Africa, from the *virens* group (9), with which in parts of the Transvaal it is in every respect sympatric. Specific separation of *pallida* is supported by the peculiar relation between its dimensions and the environment.

The foregoing conclusions leave unsolved, and indeed help to produce, the problem of the specific allocation of the montane *Zosterops* of East Africa and Abyssinia. In the first place, it has been throught best to regard the *Zosterops* of Mbulu, Kilimanjaro, North Pare, Chyulu and Teita (Map 6) as conspecific with each other and with the *Zosterops* of the eastern Kenya highlands—that is, *mbuluensis*, *eurycricota* and *silvana* with *kikuyuensis*. The last form has been shown to meet *jacksoni*, typically of the western Kenya highlands, on the north end of the Aberdares, in circumstances that suggest they are not conspecific. However, the birds of South Pare (*winifredae*) share characters of *mbuluensis* on the north and of Usambara birds on the south, in such a way that they all seem to be conspecific. Thus at three removes *kikuyuensis* would be conspecific with the very different-looking Usambara birds, which we were forced (see (4) above) to regard as representatives of *stierlingi* and hence as conspecific with *senegalensis*. This last is the same conclusion as was reached for *jacksoni* in (2) above. It follows that both *jacksoni* and *kikuyuensis*, believed though they are to meet without hybridizing, would both be of *senegalensis* stock. However, their derivation would be at so many removes and by such divergent routes that they might well behave to each other as members of separate species—*cf.* the Great Tits, *Parus major*, of eastern Asia (Mayr, 1947).

A further question is the status of the Abyssinian highland birds (group 6 above). They, too, have a high beak/wing ratio and their yellow-bellied form is so like Kenya highlands birds that it is difficult to believe that it is specifically different. Moreover, there is no difficulty in postulating colonization of the Abyssinian highlands from those of Kenya. This would make also the Abyssinia highlands birds conspecific with *senegalensis*, the nominate form of which impinges on them near Lake Tana. In this case the two forms concerned are so dissimilar in colour, size and proportions, that interbreeding would be most unlikely, whether they are anywhere genetically sympatric or not.

An alternative solution of the East African montane problem would be to make a specific cut, not warranted on morphological grounds, between the South Pare *winifredae* and the North Pare *mbuluensis*. This last, with *eurycricota* and *silvana*, would then form with *kikuyuensis* a polytypic species distinct from *senegalensis* (and *jacksoni*). This would raise a new problem—which species should the Abyssinian highland birds be attached to?

On the whole it seems preferable to adopt the first solution. The specific arrangement of the continental birds is, then, the following, as sketched in Map 1, all the species being polytypic except the first. *Z. pallida* occupies part, *Z. virens* the remainder, of South Africa, *Z. abyssinica* the lowlands of north-eastern Africa, *Z. senegalensis* the whole of the rest of Africa, being purely highland from Tanganyika to Abyssinia.

In considering the relationship of these continental species with those elsewhere there are, as usual in such cases, no guides except morphological characters. In fact with these *Zosterops* no logical solution is possible. On the one hand, there is no compelling reason, morphological or other, to follow current practice and keep either Madagascar or Indian birds as species distinct from African, but for convenience the present arrangement is certainly better maintained. Again, it seems reasonable to keep the *Zosterops* of São Tomé and Principe as a separate species, but their only important character is that they have so much less yellow pigment than their mainland neighbours. In the Indian Ocean also the distinctive Pemba *Zosterops* (*vaughani*) is better kept as a species than attached to *senegalensis* on chance, but there is no objection to this being done with the less distinctive *kirki* of Grand Comoro. *Z. mouroniensis* must, since it occurs in the same small island, be treated as a monotypic species, though its difference from *kirki* is no greater than that between typical *senegalensis* and a dark *stuhlmanni* (from near Lake Victoria). A different problem is posed by the red-flanked birds of Mayotte and of the Seychelles. Though they are separated by hundreds of miles of ocean, the extreme peculiarity that they share qualifies them as conspecific. Again, each of the species on Mauritius (*curvirostris* and *borbonica*) has a representative on Réunion. Finally, the peculiar grey *modesta* of the Seychelles must be kept as a monotypic species.

At the generic level the only separation maintainable is for the four highly aberrant birds in the Gulf of Guinea (*Speirops*).

Considerations of space make it impossible to embody the foregoing views in a formal classification in this study, which is in any case primarily one of variation, but the classification is to appear in the appropriate volume of Peters' *Check List of the Birds of the World*. It will use only those trinomials which appear in the sectional summaries of Parts 4 and 5 above.

Any discussion of the way in which the present state of these Zosteropidae came about could only be speculative and is better avoided. Even if the above view of the birds' relationships is sound, we know too little about the geological and climatic history of the African continent (Moreau, 1952), we do not know whether the first African *Zosterops* was evolved in the continent or was an invader from the east, and finally we have no idea at what stage in Tertiary history the family appeared in a recognizable form. Points of general interest are the marked variation, even though only subspecific, on East African mountains that are very close together, and the widely different types of divergence that characterize the insular Zosteropidae of the Gulf of Guinea and the Indian Ocean respectively.

Although the history of the western Zosteropidae remains inscrutable, the attempt to elucidate their relationships has a value of its own because it has brought into prominence a number of important evolutionary principles. The African *Zosterops* turn out to be a case in which, from the biological view-point of the species, the "morphological" criteria prove to be thoroughly fallacious: there is reason to believe that some of the most dissimilar birds are the most closely related and that some of those which look most alike belong to different species. Moreover, thanks especially to the statistical analyses, it has been shown that correlation takes place in relation to environmental factors to a hitherto unsuspected degree, in a manner that is both direct and highly complicated. Finally, these Zosteropidae provide outstanding examples of the manner in which birds may respond to insular life and among them beautiful and varied cases of "double invasion" of small islands.

SUMMARY

The Zosteropidae occurring in the Ethiopian Region and on Indian Ocean islands are discussed. A main difficulty in their classification has always been the delimitation of the species. This has hitherto been based almost entirely on shade of plumage, but the group is one in which morphological characters are particularly fallacious. Trinomial nomenclature is regarded as a troublesome expedient to be used primarily as a clerical convenience and sparingly.

The colour of *Zosterops* plumage often conceals pigment differences. Microscopical examination has shown that, in accord with Gloger's rule, dry-country populations usually have only brown melanin, though populations with only black melanin occur in all climates. But South African birds carry both types of melanin, and within what has always been regarded as a single subspecies the individuals in drier localities have a higher proportion of brown pigment than those in more humid.

The absence or presence of yellow pigment on the belly is regarded as not necessarily a specific character, as hitherto accepted in the classification of African *Zosterops*, but seems to have a simple genetical basis.

Wing-length in the continental birds is found on statistical analysis to be correlated positively and independently with increase in altitude, with reduction in minimum temperature of cool season and also with rise in maximum temperature of hot season. (The altitude-effect is presumably through the reduced air-pressure.) These results are discussed so far as is possible in the absence of data on weight. The minimum-temperature effect is in accord with Bergmann's rule but the maximum-temperature effect is not, and it is difficult to suggest how it operates. Tail-length and beak-length are closely correlated with wing-length, and, moreover, the tail/wing ratio increases as the wing lengthens. This seems to be correlated with minimum temperature and may be merely one aspect of the general lengthening of body plumage. While in these various correlations certain populations are somewhat aberrant, there are no discontinuities in bodily proportions so striking that they are cogent arguments for specific distinction.

The variation that takes place in the *Zosterops* of Africa is described in six geographical sections. But much of it is clinal, in close correlation with climatic factors, and convergences take place. Finally, on "biological" grounds, it is provisionally concluded that most of the *Zosterops* of Africa belong to a single polytypic species, which includes some of both the lightest (yellowest) and the darkest (greenest) birds. In East Africa this species becomes purely montane, islanded in another species; and the montane populations, though all occupying similar environments and separated by only a few miles, consist of several that differ strikingly in plumage.

The Gulf of Guinea insular Zosteropidae show several examples of double invasion, with gigantism and various other divergences from the normal. The *Zosterops* of the Indian Ocean islands are on the whole less aberrant, showing no tendency to gigantism, even among "first invaders", and the most peculiar are the Mascarene species.

Information about the past history of the Zosteropidae and of the geography and ecology of the terrain occupied is altogether insufficient for the origin of the present situation to be discussed.

APPENDIX 1

MISCELLANEOUS NOTES

NOTE 1. The following are examples of what appear to be slight, but confusing, changes in plumage colour of *Zosterops* specimens.

(*a*) Before describing the *Zosterops* of the Chyulu mountain forests as *chyuluensis*, van Someren referred a series to me for my opinion as to their distinctness from *Zosterops* of other neighbouring mountains. I had no hesitation in agreeing with his view that the Chyulu birds merited a separate name. Now that the specimens are some twenty years old, however, they look so like the neighbouring *mbuluensis* that when series are mixed not all of them can be separated (on slightly darker plumage).

(*b*) Lynes (1934) separated his birds from the contiguous highland areas of Iringa (*ca.* 5,500 ft.) and Njombe (*ca.* 6,500 ft.) into *Z. senegalensis niassae* and *Z. virens stierlingi* respectively. All that can be said of his specimens today is that on the whole the latter series averages a trifle darker than the former.

(*c*) Gyldenstolpe (1924) named all his series from Kivu *scotti* except a single one from the lake shore, which he kept as *reichenowi*. To-day I cannot pick out that specimen from the others.

NOTE 2. Two birds of ordinary *Zosterops* type, but devoid of yellow pigment, were described by Tristram from Madagascar. *Z. praetermissa*[1] owed its appearance to soaking in alcohol (A. & E. Newton, 1888), but the other, *Z. hovarum*, has been universally accepted as naturally grey. The type of the latter cannot now be found in the Liverpool Museum (Mr. R. Wagstaffe, *in litt.*), but Delacour (1932), who examined it about that date, stated that it differed from *Z. maderaspatana* in nothing but colour. There is, then, no reason to believe that *hovarum* was anything but an individual abnormality. It is curious that while the Newtons (*op. cit.*) stigmatize the plate of *hovarum* in *Ibis*, 1887, as inaccurate (they do not say in what respect), Delacour (*op. cit.*) comments that " la planche de l'*Ibis* le represente très exactement ".

Probably another such individual abnormality is the type of Büttikofer's *Z. obsoleta*, a unique specimen with the same dimensions and locality as *Z. demeryi*. The upper surface is given as ashy grey with a very faint olivaceous tinge and the whole lower surface dirty white. From South Africa there is a sight record (Urquhart, 1954) of a *Zosterops* with a " typical white eye ring " but the " entire plumage black ". It is not know whether the usual yellow pigment was present, masked by the excess melanin, or not.

Partial asymmetrical loss of yellow pigment, which has in at least some of the specimens been shown not to be an artifact (Dr. A. J. Marshall, *in litt.*), appears in individuals of four different forms in the British Museum, from Anjouan Is., Grand Comoro, Southern Rhodesia and the Orange Free State. Van Someren (1916) reported a more elaborate abnormality in a Uganda bird, " a greyish mantle and a wide buff-coloured band across the chest ".

NOTE 3. In the beautifully graded series of presumed hybrids between the yellow *gallio* and the grey *buxtoni*, which Dr. G. C. A. Junge has kindly lent me from Leiden, there is the widest possible range of intermediate variation, which seems clearly multifactorial. Here the two parent forms, with bellies that are light clear grey and bright yellow respectively, should certainly provide hybrids obvious on inspection. Nevertheless, intermediates are by no means all easy to detect on colour and the slight size-difference between *buxtoni* and *gallio* ; the nature of most intermediates showing any grey is clear, but specimens from the *gallio* end of the series of intermediates are more difficult. Here it is necessary to assess the differences in intensity of yellow, an operation often difficult in the museum (and far more so in the field). In fact the first series sent on loan from Leiden contained only intermediates of yellow types and both Dr. Cain and I felt that the evidence for their intermediacy was not very cogent. All doubts disappeared when the birds towards the grey end of the series could be assembled with them.

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[1] The word *Zosterops* is treated throughout as feminine (see *Bull. Brit. Orn. Cl.* **75** (1955) : 44).

NOTE 4. Zedlitz (1911 : 56) thought his bird shot in March at the sources of the Mareb was a young *poliogastra* in full winter dress and noted that it was hardly distinguishable from *abyssinica* in full breeding dress. There seems, however, to be no evidence for any such marked seasonal differences as Zedlitz suggested. Thanks to a loan from Stockholm Museum I have been able to examine the specimen in question. It is sexed as male juv., a point that cannot be checked, especially at the whole back of the skull seems to be missing. With wing 56, tail 40, the bird is within the size-range of *abyssinica* but is too small for *poliogastra*, and its beak is brown, a colour strictly characteristic of the *abyssinica* of Eritrea and Abyssinia. On the other hand, the bird shows an approach to *poliogastra* in being slightly greener than most *abyssinica* (and particularly than the two that Zedlitz shot a few days before), in having a little more yellow on the forehead (but not as much as in typical *poliogastra*) and in having the yellow on the throat stronger than it is in *abyssinica*.

NOTE 5. Neumann described *schoana* (type-locality Abuye, Shoa, N.W. of Addis Ababa) as differing from *kaffensis* in having duller upper parts, less yellow on the belly and narrower eye-ring than the yellow-bellies further south (*kaffensis*). On the whole the specimens in the British Museum support this, but better series, well prepared, are desirable. The four specimens available from Dangila and Wanbera (S.W. of Lake Tana) are rather intermediate. Mr. C. M. N. White, who kindly examined these specimens with me, agrees. For simplicity of discussion in the text all the highland yellow-bellies are referred to as *kaffensis*.

Friedmann (1937) showed the range of *schoana* as extending far to the south-east, across the Rift Valley, but there appears to be no basis for this extension. He agrees (*in litt.*, 1951).

NOTE 6. Neumann (*Bull. Brit. Orn. Club*, **21** : 60) claimed that the northern *poliogastra* (type-locality Simien, north of Lake Tana) have no more yellow on the head than a superciliary stripe, while those further south have yellow foreheads, and on this " distinction " he described *erlangeri* from Gadat in Gofa. He claimed that the " superciliary stripe " is much exaggerated in the coloured plate of *poliogastra* (*Ibis*, 1861), which is in fact altogether too brightly yellow and clear grey, but he used the term " superciliary " mistakenly, instead of supra-loral.

It appears that Neumann did not allow sufficiently for individual variation. It is true that a Simien specimen (lent me by the Leiden Museum) has very little yellow on the forehead, but the whole plumage is abnormally deep olive green. Other northern birds, e.g. from Eritrea and Dongolo, have as much golden yellow on the fore part of the head as any in the south of Abyssinia. I conclude, as did Ogilvie-Grant (1913 : 595), that there is no consistent geographical variation in the plumage of *poliogastra* and that *erlangeri* is a synonym.

NOTE 7. The locality " Keren " for *abyssinica* in Zedlitz (1911), and for *senegalensis* (" *aurifrons* ") in Reichenow (1903), may not be critically exact. But Bahr Dar at the south end of Lake Tana has been given by Moltoni (1940) for both *senegalensis* and *abyssinica* and, moreover, the British Museum has a specimen of *senegalensis* from the Unfras R., which is only a few miles away along the shore.

NOTE 8. In the British Museum series of *omoensis*, southwards from the northernmost point of the Omo R., the underparts vary from nearly white with yellow wash on the middle line, to pale grey washed isabelline, and almost pure grey. Kunkur birds (coll. Cheesman) are greyer, not so yellow-green on the back as any of the nine other *omoensis*, and are purer darker grey below than any others available. Yet Amadon *in litt.* reports that one of them agrees well with the type of *omoensis*. The habitat of the Kunkur birds is not certainly known ; the area is covered with acacia woodland, having evergreen trees along stream-beds (Cheesman, *in litt.*).

NOTE 9. Definite localities for *abyssinica* in Somaliland are none of them south of the mountain backbone, about 10° N., and the most northerly locality for yellow-bellies is Sillul, 8° 40′ N. But Oustalet (1886) records a yellow-bellied *Zosterops* (under the name *Z. tenella*) collected by Revoil as " capturé dans les pays Çomalis ". The route map in Revoil (1882) shows that his journeys were all north of 10° 20′ N., but since they extended to the Indian Ocean south of Cape Guardafui his *Zosterops* may have come from further east than the range of *abyssinica*, which is not known from beyond Warsangli.

Revoil's specimen is still in the Paris Museum. It is a very small (unsexed) bird, wing 51, tail 33, with plumage that is brighter and yellower than the yellow-bellies further west towards Lake Rudolf.

NOTE 10. Sclater (1930) thought that *leoninus* (*demeryi*) occurred also in Southern Nigeria, apparently on the evidence of a specimen in the British Museum from Agoulerie, just east of the lower Niger, at about 6° 25′ N. Actually this bird is not as dark as Sierra Leone and Liberian specimens. Moreover four specimens kindly collected on my behalf by Dr. W. Serle at Enugu, only forty miles east of Agoulerie and with rainfall 70 in. (but outside the forest), are typical, " yellow ", *senegalensis*. At the same time, the Lagos population (rainfall also 70 in.) may well be dark ; a single, unsexed, specimen, B.M. 1953.2.50 recently received from there, is peculiarly dull and grey. It looks like an immature, but its skull is hard.

Bannerman (1948 : 124) quoted four authors, Fairbairn, Marchant, Foulkes-Roberts and Brown, as having " reported " *leoninus* from various localities in Southern Nigeria, but as no relevant specimens could be found I made personal inquiries. All four authors have been good enough to reply and it appears that only one (Fairbairn) had collected a bird, which was, however, not authoritatively compared or kept.

In the result, there is no thoroughly satisfactory evidence that dark *Zosterops* occur in coastal Nigeria, but they are certainly to be expected in the high-rainfall belt in the extreme south, perhaps as far west as Lagos. If so, it may well be that they resemble not so much the Liberian birds far to the west, but the more strongly pigmented birds (which have been called *pusilla*) known to occur just on the eastern border of Nigeria, in the Cameroons.

NOTE 11. The lowland localities south and east of Cameroon Mt., from which I have seen small richly coloured birds are Oyem, Bitye, Efulen, Lolodorf, Sangmelima, Mbigou and Mbaika (the type of *pusilla*), i.e. all south of 4° N. It is most unfortunate that there is a lack of well-prepared material from the country just north of this, where the rainfall decreases rapidly and a transition to the yellower *senegalensis* would be expected to correspond. Two birds in poor condition from Bosum, 6° 20′ N., 16° 25′ E., including the type of *savannae*, show some approach to *pusilla*, but one from Kangala, 6° N., 14° 3′ E., shows less. Good (1953) has referred birds from Tibati (about 6° N., 13° E.) and Mboula to *stenocricota* (with which *pusilla* must be synonymized), but his description of their entire underside as " bright light yellow " shows that he is under a misapprehension as to the characters of this form. Thanks to the Chicago and Pittsburgh Museums I have been able to examine three of Good's specimens from these localities. All are much nearer *senegalensis*, having only a trifle more melanin.

NOTE 12. In northern Uganda I have seen skins from Kitgum, Yeilo (N.E. of Kitgum) and Gulu (three). They average wing 55·9, tail 39·8. The Kitgum bird and two of the Gulu are greener than typical *senegalensis*. Two birds from Kibusi Hill, Lango, 1° 54′ N., 32° 44′ E., north of the western end of Lake Kioga, are also intermediate in colour. Again, of four specimens from about 5,500 ft. on the lower slopes of Mt. Debasian (1° 50′ N., 34° 45′ E.) three are not quite so green as lakeside birds.

NOTE 13. South of Lamu and Mongeya the only specimens known from within a hundred miles of the Kenya coast are four males collected in 1900 by Doherty in the " hills 10 miles west of Mombasa " (Carnegie Mus., Pittsburgh). These hills, barely 1,000 ft. high, still have vestiges of a comparatively rich, semi-evergreen vegetation and, as Friedmann (1937) has remarked, all four birds have plumage unlike any others from East Africa. They are greener, less grey, above than the birds north of the Juba, but at the same time the whole of their underside is duller, with paler yellow on the throat and more green on the flanks. Indeed in plumage, though not in size, these Mombasa birds resemble the dull birds of the Angola highlands more than any others. Compared with others in eastern Africa they suggest the mountain forest birds of the Usambara, with both melanin and carotenoid reduced, rather than the *flavilateralis* of the Kenya savanna country. It seems possible that these Mombasa birds belong to a small population sedentary on the ecological island of these hills ; and if so it is regrettably possible that it may have been wiped out.

No specimen of *Zosterops* from Tanganyika Territory or Portuguese East Africa east of the line Usambara Mts.–Uluguru Mts.–Iringa Highlands–Songea Highlands appears to exist in collections except one from Masasi : but R. M. Bell (*in litt.*, 1951) collected a *Zosterops*, which was not retained, at Liwale, 9° 47′ S., 37° 58′ E., on 16th June, 1940. Although there have been a number of observers in the coastal strip in question I have been able to find no sight records, published or unpublished, except that of Haldane (1946) of a single bird " in thick bush along the Rufiji " River, which must I think be regarded as questionable.

NOTE 14. A number of small mountains rising to between 4,000 and 5,000 ft. that are eastern outliers of the Kenya Highlands, such as Mutha, Endau and the Kimatheni ridge, remain to be explored : and in northern Tanganyika this applies to Gelai and a few little mountains in northern Masailand west of the Pares. It is surprising that no montane *Zosterops* has been taken anywhere in the south-eastern Kenya Highlands, especially the Machakos district which must have been sufficiently wooded in the " early days". On Sagala Mt. (Ndara) just east of Voi vestigial forest resembling that inhabited by *Z. silvana* on the neighbouring Teita Hills seems to contain no *Zosterops* (A. Forbes-Watson, *in litt.*), although this bird reappears on Kasigau Mt., some forty miles further from Teita.

NOTE 15. Birds from the Yala River area, from which van Someren described *yalensis*, are hardly represented in the British Museum, but I have been able to examine thirty-seven specimens (nearly all lent by American museums), labelled " Yala R.", Kakamegoes, Kaimosi, Lerundo, Kakamega Road, K'brass and Lucosi. All these except K'brass, which cannot be fixed, are close to 0° 10′ N., 34° 55′ E.—about fifty miles north and north-west of Kisumu. Westwards from this there is a belt of country nearly 100 miles wide from which it seems that no *Zosterops* is known. The Yala birds are variable, but they certainly average yellower above and below, with less deep green on the flanks, than *jacksoni*. Some have sharply defined yellow foreheads like *jacksoni*, others more indefinite foreheads, like *stuhlmanni* of Lake Victoria. When Yala birds are mixed with a series from Uganda and Ruwenzori, and the darkest birds are picked out, they prove to come from Ruwenzori and the Yala ; the lightest are from the Entebbe neighbourhood and the Yala.

Nothing seems to have been recorded of the Yala birds in life except that van Someren in describing *yalensis* mentioned that they were found in " parkland ". This is the habitat in which *stuhlmanni* is often found.

NOTE 16. The characters by which Hartert (*Nov. Zool.*, **34** (1928) : 207) distinguished *somereni* (Mt. Kenya) from *kikuyuensis* do not hold good, as Friedmann (1937 : 373) has already noted.

NOTE 17. *Z. kulalensis* is known only from the small series collected by Mr. J. G. Williams. The two females labelled as " subadult " differ noticeably from the males and from the single adult female in the smaller amount of yellow throughout. This is particularly noticeable on the underparts, where the throat is greenish rather than yellow and there is no trace of yellow wash in the centre of the grey belly.

NOTE 18. Ketumbeine and Longido specimens are generally rather dull in colour, without strongly golden foreheads. A single specimen is known also from Oldonyo Erok, an immature, which is particularly dull-coloured, and has an eye-ring smaller than typical *mbuluensis*. The Chyulu birds (*chyuluensis*) are just distinguishable from *mbuluensis*, on average, having a little less melanin on the underparts, but the name is not worth retaining.

NOTE 19. I have been able to locate only two of the Bwamba birds on which the van Somerens (1949) based their remarks. They are females (Chicago 199163–4) from 2,500 and 3,000 ft., hardly distinguishable from the Medje birds, but perhaps with a trifle less carotenoid, with less contrast below than the Ituri group of birds and with wings 55 and 56. They are at the top of the size-range of this group and at the bottom of the size-range of *stuhlmanni*—as might be expected for their geographical situation. It may be expected that when a good series from Bwamba can be studied it will be found to be transitional between *stuhlmanni* and *toroensis*, probably with high individual variation.

NOTE 20. Specimens in point are Neave's dark birds from " Bunkeya R." and " near Lufupa R." (near Elizabethville, in the Katanga). Most workers have allocated these individuals to the species *virens*, while all the other birds from Katanga and on its borders, being yellow, were treated as *anderssoni*. Chapin, who has kindly also examined these specimens at my request, agrees that they are best regarded as individual variants.

NOTE 21. These remarks are based on twenty-seven specimens from the highlands (4,170 ft. upwards) and ten from the Vila Salazar–Quicolungo area. Chapin (1954) notes that specimens from Pungo Andongo and Canhoca (i.e. close to the two preceding localities), which I have not seen, are " very like *anderssoni* ", which implies that they have more carotenoid than the highland birds—a finding in agreement with mine. Those referred to by Monard (1934) from Indungu (50 km. S. of Vila da Ponte) and Kalukumbe cannot be traced (Director, Chaux-de-Fonds Museum, *in litt.*). Paris Museum possesses a specimen C.G. 1908 : 487 Mission Vasse labelled " Benguella ", also a fairly large (wing 60), dull-coloured bird, but it is uncertain whether it came from the coast town or from somewhere in the extensive Benguela province (which has included the highlands under discussion). If any *Zosterops* exist on the dry coastal belt of Angola, where the rainfall is as low as 10 inches, it would be extremely interesting to compare them. But none seems to have been recorded from there, nor from the neighbouring north coastal zone of South West Africa.

NOTE 22. Bangs and Loveridge described *sarmenticia* from Igale, in the Poroto and Rungwe Mts. at about 6,000 ft., as larger than *stierlingi*, and more richly coloured, with bigger beaks. I find that the birds from these mountains average barely 1 mm. longer in wing than either the dark Nyasaland birds or the dark birds from the rest of south-western Tanganyika Territory ; and I can see no difference in the beaks. But Poroto and Rungwe birds certainly are a trifle more strongly pigmented than any others, there being a specially rich contrast on the underside between deep green flanks and chrome-yellow centre of belly. Specimens which approach these most nearly come from (*a*) on the south the nearest mountains in northern Nyasaland, Nyankowa, Mugesse (Masukus) and the Nyika, (*b*) Ukinga, just east of Rungwe, and Dabaga, on the wet eastern edge of the Iringa plateau.

NOTE 23. The following names have been given to *Zosterops* in southern tropical Africa : *kasaica* Chapin (1932), from the Kasai, S.W. Belgian Congo ; *quanzae* de Schauensee (1932), (upper) Cuanza R., Angola ; *anderssoni* Shelley (1892), Elephant Vley (extreme northern S.W. Africa) ; *sarmenticia* Bangs and Loveridge (1931), Poroto Mts., S.W. Tanganyika Territory ; *stierlingi* Reichenow (1899), Iringa, S. Tanganyika ; *niassae* Reichenow (1904), Songea, S.E. Tanganyika ; *tongensis* Roberts (1936), southern P.E.A. No difficulties arise about the use of the first two names for the small, richly coloured, birds of the S.W. Belgian Congo and the large, dull, birds of the Angolan highlands respectively.

As stated, south of these the birds of the non-evergreen country extend from the Atlantic to the Indian Ocean, becoming slightly duller and greyer in the south-eastern Belgian Congo, and slightly greener in the east, as Portuguese East Africa and Zululand are approached. For these latter birds the name *tongensis* is available, but since no range could be assigned to it and the difference is so small, it is preferable to retain *anderssoni* throughout. Similarly, this name may be applied to the Songea birds, which cannot consistently be distinguished from Rhodesian. Thus *niassae* also becomes a synonym of *anderssoni* as Mackworth-Praed and Grant (1945) have already concluded.

It remains to decide on a name for the dark birds. The type of *stierlingi*, labelled as coming from Iringa, is a poor specimen, differing from the type of *niassae* only in being a little greener. If it came from the neighbourhood of Iringa township, and not from somewhere else in the then extensive Iringa Bezirk, Lynes's (1933) Iringa specimens are practically topotypes. However, he preferred to call them *niassae*, because they were a trifle yellower than the birds he got further south in Njombe, which he called *stierlingi*.

The most richly pigmented population is that north-west of Lake Nyasa, called *sarmenticia*, East, north-east (including the type locality of *stierlingi*) and south the birds become less dark, but there is no clear geographical cline. The question is whether to retain both *sarmenticia* and *stierlingi*, or only the former (the extreme type but the younger name) or only the latter (an intermediate type but the older name). I follow the last course because :

(*a*) One could not delimit the respective ranges of both *sarmenticia* and *stierlingi*.

(*b*) Birds of intermediate (nearer *stierlingi*) plumage have a far more extensive range than *sarmenticia*, discontinuously (on mountains) to some 700 miles north of Lake Nyasa, as well as down through Nyasaland.

(*c*) The name *stierlingi* has been in more general use than *sarmenticia*.

NOTE 24. *Z. capensis* has been recorded by Shortridge (*J.S. Afr. Orn. Un.* **1** : 22) as irregular in appearance July–September at Hanover, C.P., which is north-east of Murraysburg, about halfway to the Orange River. As Map 10 shows, there is nothing inherently improbable in this record, but it sounds as if it refers to wandering just before the breeding season. Also no supporting specimen can be found and as the area is a critical one for the mutual ranges of grey-bellies and pales it seems better not to enter it on the map. A *capensis* record that must clearly be rejected is that of Taylor (1907) on the Transvaal–Swaziland border. He purports to have collected it there, but no specimen can be found and the identification must be a mistake. The record of *anderssoni* close to King Williams' Town by Pym (*J.S. Afr. Orn. Un.* **5** : 91) is also dismissed as an error.

Miss Courtenay-Latimer has recorded (*in litt.*) seeing both pale-bellies and greys (*capensis*) on the banks of the Vaal R., about thirty miles north of Kimberley. Further information on the occurrence of the latter form so far from their main range must be awaited.

Map 11 is based on a sketch-map compiled for me by Dr. R. M. Harwin, mostly from unpublished information. Additional records have been incorporated from Mr. J. Last, Dr. G. Rudebeck and specimens in the British and Transvaal Museums. Since Map 11 was drawn it appears that pale-bellies are altogether more uncommon than green-bellies at Pretoria and probably also the more uncommon of the two at Johannesburg. Also Vaals have been reported from Heidelberg.

NOTE 25. The only (5) specimens from Potchefstroom, Gaberones, Matlapini and Rustenburg are all rather dull and pale. Also, seven specimens recently collected by Dr. G. Rudebeck at Blouberg, at about 23° 00′ S., 28° 55′ E., show the same characters, though only about fifty miles west of the Zoutpansberg, where the *Zosterops* are " normal " *virens*. Although evergreen forest of a dry type occurs in both mountains the Blouberg climate is drier than the other, for the mission stations at its southern foot have mean annual rainfall of only 21·7 and 27 inches compared with 44 at the south foot of the Zoutpansberg.

NOTE 26. British Museum specimen No. 76.5.23.921, classified as *pallida*, bears a note on the label that it is the specimen listed in *Ibis*, 1869 : 290 as *capensis*. The collector was Ayres and the locality " Transvaal ", a country from within 100 miles of which no grey-belly has been authentically recorded. The specimen differs from normal *pallida* in having upper parts darker and more olive, yellow on throat stronger, and entire underparts devoid of whitish. Instead the breast is greyish and the belly the same warm, rusty, brown as the flanks. There is some yellow on the forehead—a characteristic of *pallida* and *atmorii* (but not *capensis*)—and if the locality had been anywhere in the north of the Cape Province the specimen would have been accepted as a hybrid.

NOTE 27. There has been some inadvertent misrepresentation of these Gulf of Guinea birds in the text and in the figures in Bannerman (1948) :

(1) The measurements (wings 58–62, tails 45–49) ascribed to *Z. f. ficedulina* on p. 130 must be due to a clerical error ; in fact Principe birds are not bigger than the São Tomé (see Part 2 of Appendix 3).

(2) The black of the lores of *griseovirescens* is marked under the eyes, but does not continue behind them as shown in fig. 34.

(3) Fig. 36 of *leucophaea* is misleading : both in the museum and in the field (D. W.

Snow, personal communication) this looks to be a bird with a whitish head, with which the white eye-ring does not contrast.

(4) The Annobon bird is not " the largest white-eye of the genus *Zosterops* ", as stated on p. 131. In Africa it is exceeded by some Abyssinian and South African populations, as shown in Appendix 3.

(5) The green *Zosterops* from Fernando Po, described by Bannerman as *poensis*, is, as Bates (1911), Serle (1950) and Amadon (1953) have all concluded, not distinguishable from the Cameroon Mt. *stenocricota*. The slightly larger dimensions of the Fernando Po birds (compare Part 2 of Appendix 3 with population 21 in Part 1) are unexpected in view of the greater height of Cameroon Mt., but the average altitude from which the available Cameroon birds came is only 4,000 ft. and that of the Fernando Po specimens (which is unknown) may not be comparable.

(7) Colours of soft parts have in the past of necessity been derived from dried specimens, in the absence of details on collector's labels. Data recently provided give :

For *melanocephala* (W. Serle) : beak and legs both fleshy white to creamy white.

For *lugubris* (D. W. Snow) : beak yellow brown, darker above ; legs, flesh.

For *leucophoea* (D. W. Snow) : upper mandible dark grey, lower, whitish ; legs and feet pearl grey with yellow soles.

The beaks of *ficedulina* and *feae* differ markedly in colour, at any rate in the skins, the former being dark horn above, paler below, and the latter whitish tipped blackish.

NOTE 28. Stresemann (1948) is prepared to keep three of the abnormal birds in *Speirops* but regards the remaining one, *brunnea*, as " closer to the ordinary type of *Zosterops* ". He points out that *brunnea* has a longer tail, more slender beak and different colour pattern from *Speirops lugubris*. In colour, however, *lugubris* differs no less from another *Speirops*, *leucophoea*, and its shortness of tail is a character of some otherwise " normal " *Zosterops*. Also, *brunnea* is so far from being an " ordinary " *Zosterops* that hesitation must be felt about including it in that genus. And, on the whole, in view of the uncertain phylogeny of these Gulf of Guinea birds, no violence is done, and practical convenience is served, by keeping all four abnormal birds in *Speirops*.

It may be added that *Speirops brunnea* is known from only two specimens. The type (not sexed) was described by Salvadori as having wing 62, tail 50. The Berlin bird, also not sexed, Stresemann (1948) reported as having wing 66, tail 54, but on remeasurement (*in litt.*) 65/55.

NOTE 29. While the brightest *griseovirescens* is only grey-green, some specimens (especially worn birds, including one noted on its label as " nesting ") are so devoid of lipochrome that on the upper parts the green is limited to a tinge on the upper tail-coverts and the under tail-coverts are practically white. There is also much variation in the colour of the belly and flanks, some being a warm brown (correlated with the greener type of upper parts), others very pale.

NOTE 30. My conclusions about the Madagascar birds, based on the British Museum series, have been reached independently from those of Salomonsen (1934*a*, 1934*b*) and Rand (1936). Although the series I have seen is smaller than that available to Salomonsen, it suggests no such clear distinction in size between *analoga* and the other populations as he thought. It is true that the high-level (Manjakatompo) birds I have measured have wings 59–63 mm. and the smallest *Zosterops* in Madagascar 52–58, but two from Iampasika, at an intermediate level, have wings 59 and 60 and three from lower altitudes elsewhere in the island 59.

NOTE 31. The plate of *Z. comorensis* in Shelley (1900) is not quite accurate in that it makes the bend of the wing too yellow and shows a sharp demarcation between yellow throat and green side to head. This would be correct for the Madagascar birds, but the *comorensis* skin appears to have ear-coverts and cheeks greenish yellow, not green, and hence not contrasting with the throat.

NOTE 32. *Z. mouroniensis* seems to be represented by only three very old specimens, two mounted in Paris and one (without collector's name) in Berlin which was at one time mounted, Thus at least one of the four birds collected by Humblot (Milne-Edwards and Oustalet, 1888) is unaccounted for. Thanks to Professor Stresemann I have been able to examine the Berlin specimen. It has upper parts a dingy olive-green, underparts a greyish olive yellow (including the under tail-coverts and thighs). It is altogether much darker and less yellow than as figured in Plate 5 (*ibid.*), but at least some of this effect may be due to age and dirt. Its wing measures 63 mm., tail 45, tarsus 22 (beak damaged). Professor Berlioz has kindly measured the mounted specimens in Paris for me and finds wings 60 and 64, tails 50 and 52. Milne-Edwards and Oustalet (1888) gave wing 66, tail 57. The name of the bird is derived from Mouroni, the (low-level) capital of Grand Comoro, but it is not clear that it was obtained there, as Shelley (1900) states.

NOTE 33. Vesey-Fitzgerald (1940) found no *Zosterops* on Marianne, but specimens in the British Museum show that it persisted there as late as 1888. Its extinction may have resulted from the clearing of the jungle for coconuts that Newton (1867) heard was intended. There appears to be no concrete evidence to support the record of *semiflava* from Praslin Island (15 sq. miles) by Shelley (1900) and Sharpe (1909): and the mention of *semiflava* by Newton (1867) on Praslin, Silhouette (8 sq. miles), La Digue (4 sq. miles) and Mahé, is in every case tentative or by local report.

NOTE 34. *Z.* (*Malacirops*) *e-newtoni*, described by Hartlaub from Réunion, was not decisively rejected by Sclater. Gadow (1884) may, as A. & E. Newton (1888) claimed, have had inadequate material at that date for his statement that *Z. e-newtoni* and *Z. borbonica* " form a perfect gradation " ; but *e-newtoni* certainly differs only in having its plumage a cold grey throughout, instead of being suffused with brown like *borbonica* ; Berlioz (1946) is convinced that it does not deserve specific status ; and it is incredible that in the island of Réunion there should be two *Zosterops* of identical size and proportions (in addition to *haesitata*). The *e-newtoni* individuals on Réunion in fact are a local abnormality that is more like the allied form, *mauritiana*, on Mauritius. *Pace* Gadow (1888) there appears to be inadequate sexed material to support the view that the female *borbonica* is browner than the male.

NOTE 35. The *Zosterops* of Gloriosa Is., described by Ridgway as *gloriosae*, is represented in the British Museum by six good skins. When mixed with a series from Madagascar they cannot be separated from the yellowest, and their measurements (wings 55–57·5) fall within the range of *maderaspatana*. Nicoll (1906) also concluded that they were indistinguishable and it is not known on what grounds Sclater (1930) retained the name *gloriosae*. Most of the Gloriosa birds have a little yellow wash on the grey belly, and an immature female has most of the underparts washed with gamboge, together with a golden tinge on the lores. No *Zosterops* seems to have been collected on Astove ; the single one from Cosmeledo is a little yellower than Madagascar birds.

NOTE 36. *Z. völtzkowi* was originally described by Reichenow by comparison with *anjouanensis* and *comorensis* (which it seems unlikely that he can have seen), apparently on one skin and four specimens in spirit, which have of course lost all their yellow. However, four specimens obtained recently (1948) by Lt.-Col. Ph. Milon on Europa Is., while showing no consistent difference in colour or wing-length from Madagascar birds, have markedly longer tails.

APPENDIX 2

ANCILLARY CHARACTERS

Iris colour

The only *Zosterops* in which any iris-colour other than brown appears to preponderate are those *senegalensis* which extend in a belt along the southern edge of the Sahara from Senegal to Eritrea. Bates (1930) gives the iris-colour of West African birds as " light grey " and he is supported by the particulars on the labels of most of the B.M. specimens from Cameroons westward ; yet Bannerman (1948) gives " very pale yellowish brown " for West African birds, and Reichenow (1903) " dark red brown ". Certainly the iris-colour of immature birds in West Africa is brown (see especially two immatures from Portuguese Guinea with irises noted by Ansorge as " brown ochre "). Of exceptional adults, W. P. Lowe got a female with " brown " iris at Bathurst, in the Gambia, Shuel a female with " brownish " at Zaria in Nigeria, and Bates himself a male in Bornu with " very light yellowish brown " and a male with " brown " in the Cameroons. At the eastern end of " *senegalensis* " Butler and Lynes recorded iris-colour of Roseires and Darfur birds respectively as grey, while an unsexed bird collected by Bohndorff at 8° N., 26° E., S.S.E., of Lynes' bird, had " full brown " iris and a Kajo-Kaji bird collected by J. H. Miller " hazel ". Again, among the series of Uganda *stuhlmanni*, typically with brown iris, there is one with iris noted as " white ". Still more remarkably, in a series of eight specimens all apparently adult, from Melsetter, Southern Rhodesia, the iris colours are noted variously as yellow, light yellow, grey and brown (of several shades).

Beak colour

Throughout Africa the beaks are black, except in two Abyssinian populations, *omoensis* of the southwest and *abyssinica* of the east, which have the beaks brown. However, the populations of *abyssinica* that live further to the south-east, in Somaliland, and are otherwise similar to the others, have black beaks. All the insular birds of the Indian Ocean also have black beaks ; it is only the otherwise highly aberrant birds of the Gulf of Guinea islands and Cameroon Mt. which have strikingly different beaks—whitish.

Leg colour

All the forms whose leg colour is recorded on labels have it more or less grey—brownish-grey to blue-grey—except two from the Gulf of Guinea that are in other respects highly aberrant (genus *Speirops*). These have pale flesh-coloured legs.

Feathering sequence of the nestling

A peculiar condition of head-feathering has been recorded (Moreau and Moreau, 1939) in nestlings of the Kilimanjaro and the Usambara mountain-forest *Zosterops*, two forms the adults of which are as unlike as any of those belonging to that habitat. Two young Kilimanjaro *Zosterops* about two days before they left the nest had the back, wings and crown fully feathered, but the forehead was only in quill, while " the lores, together with a strip over and under the eye were bare. There was no sign of the white eye-ring, even in quill." Again, in Usambara nestlings which had the feathers on the hinder half of the crown full-grown " the entire forepart of the head was practically naked ". Since no similar records had been traced elsewhere it seemed that this might possibly be a character of taxonomic significance and attempts have been made to learn something of its geographical occurrence.

In Nyasaland Mr. C. W. Benson has kindly given me details of two broods of advanced nestlings regarded as conspecific with Usambara birds. In one brood the retardation of feathering on the fore part of the head was as in the Usambara birds ; but in the other brood feather-sheaths were showing on the lores. Dr. Chapin has recently sent me a nestling from the Kivu which shows a somewhat intermediate condition. It is fully feathered (tail and wings still very short), but the lores and the rim round the eye, which would in the adult be occupied by the white eye-ring, are bare. The only other African *Zosterops* for which I have been able to get any information is the (grey-bellied) Cape Town bird ; Mrs. M. K. Rowan (*in litt.*) has collected information that the head-feathering is complete in the nestling stage.

Delay in head-feathering seems to be widespread in the genus *Zosterops*. Davidson (1952) has noted that young New Zealand *Zosterops* (*lateralis*) on the day before leaving the nest had " a little bare patch on the top of the head and round the eye " ; the photograph of newly fledged birds ascribed to *simplex* (from somewhere in south-eastern Asia) in Schmitt (1931) appears to show the forehead and the surroundings of the eyes as naked. But Mr. E. M. Reid-Henry tells me that lowland Ceylon birds (*palpebrosa*) do not show any bareness. Also two nestling *hypoxantha* (from the Pacific), lent by Prof. Stresemann, have the head completely covered.

More critical observations are needed, but meanwhile it seems that sequence of head-feathering is probably not a useful taxonomic character.

Beaks and tongues

The beak is so readily adaptive that it cannot be expected to be of taxonomic significance. It may, however, be noted that the beaks of all the Zosteropidae under discussion are much alike, irrespective of habitat, except for special elongation in one species inhabiting Mauritius and Réunion. In general, also, the correlation between length of beak and length of wing is remarkably close (Part 3).

In connection with the present study, as many tongues have been examined microscopically as possible, and the result will, it is hoped, be published separately. All show a rather similar degree of specialization, being bifid, slightly folded so as to provide a channel (for nectar and juices), and fimbriated.

Wing formula

In all the Zosterops dealt with in this study, primaries 3, 4 and 5 are the longest, nearly equal, markedly exceeding primary 2 (by up to one-tenth of the wing-length) and somewhat exceeding primary 6. This in most forms is markedly longer than primary 2. (Primary 1 is so reduced in all forms that it does not enter into discussion.)

The biggest differences between primary 2 and primary 3 (up to 6 and 7 mm.) are found in the various highland birds of East Africa and Abyssinia, which might be expected, merely because these are the longest-winged birds. The small birds of south-western Abyssinia (*omoensis*) have, however, nearly as big a gap between second and third primaries. In general, the difference between primaries 2 and 6 varies with that between 2 and 3, though it is consistently smaller. But in each population the individual variation in these respects is great.

Two forms of African *Zosterops* are more blunt-winged than any others : both the pale-bellied birds of south-western Africa (*pallida*) and the yellow birds of the northern savanna (*senegalensis*) have the difference between the second and third primaries as little as 2 mm. in some specimens and the sixth little or no longer than the second.

From the foregoing it appears that wing-formula is not of taxonomic value. Nor does it seem to have a consistent ecological relationship. The two blunt-winged forms cited above both belong to dry country, but the character is less marked in two others of comparable environment, *abyssinica* and *flavilateralis*.

Song

Song is known to be variable in some species of birds (even to the extent of losing locally the specific characters). However, for the *Zosterops* as much information as possible has been assembled, much of it unpublished, from correspondents, in case something helpful should emerge. Especially as verbal renderings of bird-songs are difficult to evaluate, by far the most valuable information comes from the comparisons made of *Zosterops*-songs in different areas made by individual listeners. Thus :

(1) The songs of the two Nyasaland *Zosterops*, highland and lowland, were found by Benson (1948) to be identical with each other and with that of the superficially very different, grey-bellied, bird of the Abyssinian highlands, while he also once heard the same song from a Uganda bird. The four birds concerned have usually been attributed to three different species (four different subspecies).

(2) The Usambara and Kilimanjaro mountain-forest birds, which look as different as any two forms occurring in this vegetation-type, have the same song (personal observations).

(3) The South African birds, green-bellied, grey-bellied and pale-bellied, which in the past have been attributed to two, or three, different species, have all practically the same song (Mr. C. J. Skead ; Mrs. M. K. Rowan).

All the songs referred to above are described as being of Blackcap (*Sylvia stricapilla*) or Garden Warbler (*S. borin*) type and quality. Something of the sort is probably very widespread in the Zosteropidae, for in New Zealand *Z. lateralis* sings like a Hedge Sparrow (*Accentor modularis*)—Mr. E. G. Turbott, personal communication. It is therefore surprising to find that one Kenya form (*Z. kikuyuensis*), occupying mountain forests situated between those inhabited by the birds with Blackcap-type songs cited above, has a very different song—described by Sir Charles Belcher, a very competent observer, as about twenty repetitions of practically the same note. This may perhaps have affinities with the several songs that have been likened by observers to that of the Willow Warbler (*Phylloscopus trochilus*), in Pemba Island (off the East African coast) and on Principe Island (Gulf of Guinea)—as well, incidentally, as in Ceylon (*palpebrosa* but not *ceylonensis* : Mrs. C. Lushington *per* Major W. W. A. Phillips *in litt.*).

For the present purpose all that can usefully be inferred from the foregoing is that among the African *Zosterops* birds of very dissimilar appearance, which have been ascribed to different species, have similar songs. In such cases identity of song would support arguments, put forward on other grounds, that the birds concerned were conspecific, but the song character alone could bear no weight for or against close affinity.

APPENDIX 3

DIMENSIONS, ETC., OF VARIOUS POPULATIONS OF ZOSTEROPIDAE

Notes

(1) Names are taken from Sclater (1930) or subsequent describer, without prejudice to reconsideration. Where no name is given none has been applied to, or covers, the particular population.

(2) " Mean altitude " and " temperature " are obtained as explained in Part 3.

(3) Beak-lengths are not available for certain populations (see Part 3).

(4) Standard deviations in wings are all below 2·5 mm. (only 3 of them exceeding 2·0), in tails all below 3 mm. (18 exceeding 2·0), in beaks all below ·9 mm. (7 exceeding ·75).

Part 1. African Continental Populations

Population.		Specimens examined								
				Temperature °F.						
No.	Area and name.	No.	Mean altitude a.s.l. (ft.).	Max. (mean)	Min. (mean)	Wing-length mm.	Tail-length mm.	$\frac{100 \times \text{tail}}{\text{wing}}$	Beak-length mm.	$\frac{100 \times \text{beak}}{\text{wing}}$
	N.E. Tropical Africa									
1	Eastern Ethiopian highlands except extreme south (*poliogastra*)	54	8,000	77	46	63·9 (58–69)	48·4 (43–53)	75·7	14·1 (13–15)	22·1
2	Eastern Ethiopian highlands extreme south (round Yavello) (*poliogastra*)	11	6,000	83	50	61·5 (59–63)	47·3 (46–49)	76·9	14·1 (13–15)	22·9
3	Western Ethiopian highlands, north of Addis Ababa–Nono (*schoana*)	14	8,000	77	46	63·2 (61–65)	48·7 (45–50)	77·1	14·7 (14–16)	23·3
4	Western Ethiopian highlands Addis Ababa–Nono southwards (*kaffensis*)	29	6,500	82	48	60 (57–63)	45·1 (41–48)	75·0	14·0 (13–15)	23·3
5	S.E. Sudan and E. Eritrea below 5,000 ft. (*abyssinica*)	15	3,500	96	60	54·4 (52–56)	38·4 (36–42)	71·1	12·9 (12–14)	23·7

Population.		Specimens examined.								
			Mean altitude	Temperature ° F.						
No.	Area and name.	No.	a.s.l. (ft.).	Max. (mean)	Min. (mean)	Wing-length mm.	Tail-length mm.	100 × tail / wing	Beak-length mm.	100 × beak / wing
6	Ethiopia, eastern dry country (*abyssinica*)	16	4,500	89	57	58·3 (54·5–60)	41·8 (38·5–45)	72·0	13·3 (12–14)	22·9
7	British Somaliland (*abyssinica*)	21	4,000	86	52	57·1 (55–60)	41·9 (39–46)	73·4	13·4 (12·5–15)	23·5
8	S.W. Ethiopia lower ground (*omoensis*)	11	4,000	93	59	55·7 (54–57)	39·0 (35–41)	70·0	12·7 (12–13)	22·8
9	Imatong group of mountains, Sudan - Uganda border	14	7,000	83	47	60·0 (58–62)	42·2 (39–48)	70·0	13·3 (12·5–14)	22·1
10	Round N. end Lake Rudolf (*jubaensis*)	11	2,000	94	70	52·1 (50–54)	34·3 (32–38)	65·8	12·2 (11·5–12·5)	23·4
11	East of population 10 (lower ground S. of Yavello; (*australoabyssinica*)	14	4,500	86	61	53·6 (52–56)	36·6 (35–39)	68·3	12·1 (11–13)	22·6
12	Italian Somaliland (*jubaensis*)	17	500	98	72	51·8 (50–54)	34·2 (31–37)	66·1	11·5 (11–12)	22·2
	WEST AFRICA AND SUDAN									
13	Liberia and Sierra Leone (*leoninus*)	14	500	91	68	52·8 (51·5–54)	35·1 (33–37)	66·6	11·8 (11–13)	22·3
14	Gold Coast westwards except area 13 (*senegalensis*)	18	500	94	66	53·5 (51–55)	35·6 (33–37)	66·3	12·4 (11·5–13)	23·2
15	Nigeria and Cameroons below 3,500 ft., north of 8° N. (*senegalensis*)	23	1,500	98	63	55·9 (53–59)	37·5 (35–40)	67·1	12·2 (11–13)	21·8
16	Nigeria and Cameroons below 3,500 ft. 8°–4° 30′ N. (*senegalensis*)	19	1,500	88	67	53·7 (51–57)	36·0 (34–39)	67·0	12·5 (11·5–13)	23·1

Population.		Specimens examined								
				Temperature °F.						
No.	Area and name.	No.	Mean altitude a.s.l. (ft.).	Max. (mean)	Min. (mean)	Wing-length mm.	Tail-length mm.	$\frac{100 \times \text{tail}}{\text{wing}}$	Beak-length mm.	$\frac{100 \times \text{beak}}{\text{wing}}$
17	Sudan north of 8° N. (*superciliosus*)	15	2,000	100	62	56·1 (54–58)	38·3 (36–40)	68·5	12·6 (12–13)	22·5
18	Sudan and N.E. Congo 8°–3° N. (*superciliosus*)	25	2,000	94	64	54·6 (52–59)	37·3 (35–41)	68·3	12·3 (11–13)	22·5
19	Bamenda highlands (*stenocricota*)	24	6,000	82	59	58·7 (56–61)	38·6 (34–41)	65·5	13·5 (12·5–14·5)	23·0
20	Manenguba group of highlands	9	4,000	84	64	53·1 (51–55)	31·2 (30–34)	58·2	12·7 (12–13·5)	23·9
21	Cameroon Mt. (*stenocricota*)	13	4,000	89	69	54·2 (52–57)	33·4 (31–35)	61·6	12·1 (11·5–12·5)	22·3
22	Cameroon Mt. (*melanocephala*)	21	8,000	65	46	63·0 (61–65)	43·2 (41–47)	68·6	15·0 (14–15·5)	23·7
23	S.E. of Cameroon Mt. to 1° N. and 3° E. (*pusilla*)	12	1,000	89	69	51·3 (49–53)	31·5 (30–33)	61·4	12·5 (12–13)	24·3
	EAST AFRICA									
24	Eastern Kenya below 4,000 ft. (*flavilateralis*)	53	2,300	88	65	53·8 (51–57)	35·7 (32–39)	66·3	12·0 (11–13)	22·3
25	Eastern Kenya, dry country 4,000–6,000 ft. (*flavilateralis*)	32	5,000	83	55	55·4 (50·5–59)	37·8 (35–41)	68·2	12·2 (11–13·5)	22·0
26	Tanganyika Territory, dry below 4,000 ft. (*flavilateralis*)	34	2,500	86	60	54·3 (52–57)	36·9 (35–39)	68·0	12·2 (11–13)	22·5
27	Central Tanganyika, dry 4,000–6,000 ft. (*flavilateralis*)	30	5,000	82	53	55·2 (53–58)	38·3 (35–41)	69·2	12·2 (11–13)	22·1
28	Kulal Mt., N. Kenya (*kulalensis*)	8	6,000	81	50	62·7 (61–64)	46·5 (45–51)	74·2	15·4 (14–16)	24·6

Population.		Specimens examined.								
			Mean altitude	Temperature ° F.						
No.	Area and name.	No.	a.s.l. (ft.).	Max. (mean)	Min. (mean)	Wing-length mm.	Tail-length mm.	$\frac{100 \times \text{tail}}{\text{wing}}$	Beak-length mm.	$\frac{100 \times \text{beak}}{\text{wing}}$
29	Marsabit Mt., Kenya	12	4,000	80	57	57·5 (56–60)	41·0 (39–42)	71·3	12·8 (12·5–13)	22·2
30	Laikipia plateau, Kenya	7	6,700	79	46	62·6 (60–64)	47·0 (43–51)	75·1	13·7 (13–14)	21·9
31	Mt. Kenya 9,500 ft. upwards (*kikuyuensis*)	23	10,000	69	40	62·0 (59–66)	47·6 (43·5–50)	76·8	13·9 (13–15)	22·4
32	Rest of E. Kenya highlands (*kikuyuensis*)	95	7,500	76	46	60·6 (56·5–64)	46·4 (42–51)	76·6	13·7 (12–15)	22·7
33	Chyulu Mts., Kenya (*chyuluensis*)	14	6,000	81	50	62·0 (59–65)	47·9 (45·5–52)	77·3	14·5 (13·5–15)	23·4
34	Teita Hills, Kenya (*silvana*)	33	5,000	82	53	58·1 (56–63)	45·7 (43–49·5)	78·6	14·5 (13·5–16)	24·9
35	Kilimanjaro group (*eurycricota*)	46	6,000	80	49	61·1 (59–64)	47·7 (43–50)	78·1	14·2 (12·5–16)	23·2
36	N. Pare Mts., Tanganyika Territory (*mbuluensis*)	14	5,500	82	51	60·4 (58–63)	45·1 (40–48)	74·7	14·2 (13·5–15·5)	22·7
37	Mbulu group of mountains, N. Tanganyika (*mbuluensis*)	37	6,500	78	48	62·5 (60–67)	47·5 (43–53)	75·9	14·7 (13·5–16·5)	24·3
38	S. Pare Mts., Tanganyika Territory (*winifredae*)	12	5,500	82	51	59·1 (58–62)	43·3 (41–46)	73·3	13·7 (13·5–14)	23·2
39	Mt. Elgon, N.W. Kenya (*jacksoni*)	45	(7,000)	78	49	60·6 (58–65)	46·0 (42–51)	75·9	13·7 (12·5–15)	22·6
40	Western Kenya highlands between Elgon and Naivasha (*jacksoni*)	68	8,500	73	43	62·0 (57–67)	46·4 (42–50)	74·8	13·9 (13–16)	22·4
41	Western Kenya Highlands Naivasha–Loliondo (*jacksoni*)	17	7,000	75	48	60·6 (57–65)	46·6 (40–49)	76·9	13·5 (13–14·5)	22·3

Population.		Specimens examined		Temperature ° F.						
No.	Area and name.	No.	Mean altitude a.s.l. (ft.).	Max. (mean)	Min. (mean)	Wing-length mm.	Tail-length mm.	100 × tail / wing	Beak-length mm.	100 × beak / wing
42	Kavirondo, W. Kenya (*yalensis*)	38	4,500	86	58	58·3 (56–62)	42·3 (39–46)	72·5	13·2 (12·5–14)	22·6
43	Ukerewe Is., L. Victoria	11	4,000	83	62	58·8 (57–61)	43·9 (42–45)	74·7	12·4 (11·5–13)	21·1
44	Uganda below 5,000 ft. (*stuhlmanni*)	49	4,000	85	60	58·1 (55–62·5)	41·3 (37–44)	71·1	13·0 (12–14)	22·4
45	Ruwenzori (over 5,000 ft.) (*stuhlmanni–scotti*)	67	6,900	75	50	60·2 (56–63)	44·5 (41–49)	73·9	13·4 (12·5–15)	22·2
46	Ruwenzori, western foothills	37	4,000	86	60	57·9 (54–61)	41·3 (36–47)	71·3	12·7 (11·5–13·5)	21·9
47	Bwamba – Ituri – Beni, N.E. Belgian Congo (*toroensis*)	18	3,000	89	63	53·7 (51–56)	36·9 (34–40)	68·7	12·3 (11·5–13)	22·9
48	Highlands W. of L. Edward to 5,000 ft.	31	4,700	80	57	57·1 (54–60)	40·6 (37·5–44)	71·5	—	—
49	Highlands W. of L. Edward 5,000–8,500 ft.	10	6,800	73	51	61·5 (58–65)	46·6 (45–50)	75·7	—	—
50	Kivu volcanoes.	32	9,500	65	41·5	62·5 (59–65)	47·9 (43–51)	76·6	13·9 (13–15)	22·2
51	Kivu, lower levels	44	6,000	77	53	60·7 (58–64·5)	45·4 (40–50)	74·7	13·3 (12·5–14)	22·0
52	Mountains N.W. of Lake Tanganyika (*reichenowi*)	22	7,000	73	50	61·4 (59–64)	45·3 (41–50)	73·8	13·7 (13–14)	22·3
53	Kakanda, 40 miles west of preceding (52)	14	4,300	82	60	55·9 (54–58)	39·1 (37–41)	70·0	—	—
54	Kamituga, 25 miles west of preceding (53)	8	3,000	87	66	53·1 (52·5–54)	35·5 (34·5–37)	66·8	—	—
55	Mt. Kabobo, 5° 8′ S., west side of Lake Tanganyika	10	5,200	?	?	58·9 (56–62)	41·4 (39–43)	70·3	13·5 (13–14)	22·9

Population.		Specimens examined.								
			Mean altitude	Temperature ° F.						
No.	Area and name.	No.	a.s.l. (ft.).	Max. (mean)	Min. (mean)	Wing-length mm.	Tail-length mm.	100 × tail / wing	Beak-length mm.	100 × beak / wing
	SOUTHERN TROPICAL AFRICA									
56	Kasai, S.W. Belgian Congo (*kasaica*)	13	2,000	88	64	52·5 (51–56)	35·1 (33–39)	66·9	12·0 (11–13)	22·9
57	N. Angola; Ndala Tando–Quicolungo	10	2,500	86	58	57·2 (54–59)	38·9 (35–42)	68·0	12·9 (12·5–14)	22·5
58	Angola highlands, Benguela plateau (*quanzae*)	27	5,500	83	45	61·8 (60–66)	43·9 (39–47)	69·4	13·0 (12·5–14·5)	21·0
59	Katanga–Upemba, S. Belgian Congo (*anderssoni*)	43	4,000	88	50	59·9 (57–63)	40·8 (36·5–44)	68·1	12·9 (12–14)	21·5
60	N. Rhodesia 3,500–5,500 ft. (*anderssoni*)	51	3,800	87	48	59·4 (56–62)	41·8 (39–45)	70·4	12·6 (12–14)	21·2
61	N. Rhodesia above 5,500 ft. (*anderssoni*)	18	5,800	80	41	61·0 (59–63)	42·5 (41–46)	69·8	—	—
62	S. Rhodesia (*anderssoni*)	19	4,500	83	43	59·3 (57–62)	39·8 (34–43)	67·9	12·9 (12–13·5)	21·7
63	Nyasaland, mainly *Brachystegia* country (*anderssoni*)	48	4,000	82	53	58·6 (55–62)	39·8 (34–43)	67·9	12·5 (11·5–13·5)	21·3
64	Nyasaland and Namuli mountain forests. (*stierlingi*)	23	6,000	76	46	58·5 (57–61)	41·0 (38·5–44)	70·0	13·1 (12–14)	22·4
65	Portuguese East Africa and Zululand, 15–28° S. (*tongensis*)	56	500	90	56	56·6 (55–60)	39·2 (35–43)	69·2	12·2 (11·5–13)	21·5
66	Kungwe and Ufipa highlands, east of Lake Tanganyika.	9	6,500	?	?	60·2 (58–62)	40·4 (38–43)	67·0	12·8 (12–14)	21·3
67	Songea, S.E. Tanganyika Territory (*niassae*)	17	4,000	82	54	57·7 (55–62)	38·9 (35–40)	67·4	—	—

Population.		Specimens examined		Temperature ° F.						
No.	Area and name.	No.	Mean altitude a.s.l. (ft.).	Max. (mean)	Min. (mean)	Wing-length mm.	Tail-length mm.	100 × tail / wing	Beak-length mm.	100 × beak / wing
68	Rungwe and Poroto Mts., S.W. Tanganyika Territory (*sarmenticia*)	16	7,000	72	45	58·6 (57–61)	40·2 (38–42)	68·6	12·7 (12–13·5)	21·7
69	Rest of S.W. Tanganyika Territory (*stierlingi*)	31	6,000	75	48	57·7 (56–60)	39·8 (37–43)	68·9	13·0 (11·5–14)	22·5
70	Nguru-Uluguru Mts., Tanganyika Territory (*stierlingi*)	20	5,000	79	53	56·4 (55–60)	37·8 (35–41)	67·0	12·8 (12–13·5)	22·7
71	W. Usambara Mts., N.E. Tanganyika Territory (*stierlingi*)	31	5,000	81	56	56·1 (53–58)	39·6 (35·5–42)	70·6	12·9 (12–13·5)	22·9
72	E. Usambara Mts., N.E. Tanganyika Territory (*stierlingi*)	8	3,000	82	59	54·4 (53–57)	37·8 (35·5–40)	69·5	13·0 (12·5–13·5)	23·7
	SOUTH AFRICA									
73	Interior 2,000 ft. upwards (*virens*)	28	4,000	82	38	62·1 (60–66)	46·6 (44–52)	75·0	13·9 (12·5–15)	22·4
74	Coastal Natal and Eastern Cape Province (*virens*)	45	1,000	82	49	59·6 (56-62)	45·1 (42–50)	75·5	13·4 (12–15)	22·5
75	Zululand and S. P.E.A. (*virens*)	25	1,000	84	51	59·6 (55–62)	44·8 (41–48)	75·2	13·4 (12–15)	22·6
76	O.F.S. and S.W. Transvaal (*pallida*)	35	4,000	87	35	59·3 (56–62)	47·0 (45–50)	79·2	12·6 (11–14)	21·2
77	S.W. Africa and N.W. Cape Province (*pallida*)	25	1,000	87	44	56·2 (54–58)	44·1 (42–48)	78·4	12·4 (11–13·5)	22·6
78	S.W. Cape Province (*capensis*)	26	500	80	46	59·2 (57–64)	46·5 (45–49)	78·6	13·6 (13–15)	23·0
79	Rest of Cape Province (*atmorii*)	52	1,500	82	43	60·1 (57–64)	46·0 (42–50)	76·7	13·5 (12–15)	22·5
80	Basutoland and borders (*atmorii*)	10	4,500	77	35	64·1 (62–66)	48·5 (46–50·5)	75·8	14·0 (13·5–14·5)	21·8

PART 2. GULF OF GUINEA

Island and name of bird[1]	Wing-length (mm.)		Tail-length (mm.)		Ratio $\frac{100 \times \text{tail}}{\text{wing}}$	Beak-length (mm.)		Ratio $\frac{100 \times \text{beak}}{\text{wing}}$
	Mean.	Range.	Mean.	Range.		Mean.	Range.	
GULF OF GUINEA								
Fernando Po, *brunnea* (1)[2]	—	(65)	—	(55)	82·7[2]	—	(13·5)	20·8
,, ,, *poensis* (12)	56·1	(54–59)	35·4	(33–38)	62·8	13·4	(12·5–14)	23·9
Principe, *leucophoea* (13)	68·3	(67–71)	47·7	(46–50)	69·8	14·9	(14–16)	21·8
,, *ficedulina* (6)	52·6[3]	(51–54)	37·7	(34–40)	71·7	13·5	(12·5–14·5)	25·7
São Tomé, *lugubris* (11)	74·4	(72–77)	46·0	(48–53)	61·8	15·9	(15–16·5)	21·4
,, ,, *feae* (16)	55·2[3]	(53–56)	37·1	(33–39)	67·2	12·7	(12–13·5)	23·1
Annobon, *griseovirescens* (10)	62·2	(59–64)	48·7	(46·5–51·5)	77·6	15·8	(14·5–17)	25·4

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[1] Number of specimens examined is given in brackets. The name is taken from Sclater (1930) without prejudice to reconsideration.

[2] The only other known specimen is stated to have had wing 62, tail 50 (Salvadori, 1903). The wing/tail ratio is based on both specimens (see Note 28, Appendix 1).

[3] As most of the Principe birds available were females and the São Tomé were males or unsexed, the difference in mean wing-lengths on comparable series from the two islands would probably be less than the 2·6 mm. indicated.

PART 3. INDIAN OCEAN BIRDS

	Number of specimens examined.	Wing-length. mm.	Tail-length. mm.	Ratio $\frac{100 \times \text{tail}}{\text{wing}}$.	Beak-length. mm.	Ratio $\frac{100 \times \text{beak}}{\text{wing}}$.
MADAGASCAR AND OUTLIERS						
Madagascar below 4,000 ft.	55	54·8 (52–59)	37·3 (35–41)	67·6	13·5 (12–15)	23·7
Madagascar 4,000 ft. upwards	5	60·8 (59–63)	42·5 (39–44·5)	70·0	14·1 (13–15)	23·2
Gloriosa	6	56·8 (55–57·5)	39·5 (37–40)	69·5	13·9 (13–15)	24·6
Aldabra	4	52·1 (51–53)	38·2 (37–40)	73·3	11·5 (11–12)	22·0
Cosmoledo	1	56	36	64·3	14·0	25·0
Europa	8	55·9 (53–59)	42·4 (39–46)	75·8	—	—
COMORO ISLANDS						
Grand Comoro (*comorensis*)	1	52·5	35	66·6	12·5	23·8
,, ,, (*kirki*)	7	53·4 (52–54)	35·7 (35–36)	66·9	12·8 (11·5–13)	24·0
,, ,, (*mouroniensis*)	3	62·3 (60–64)	49 (45–52)	78·6	14·0	22·5
Mayotte	16	53 (52–54·5)	33·5 (32–35)	63·2	14·0 (13–15)	26·4
Anjouan	11	56·8 (54–58)	36·5 (33–38)	64·6	14·4 (14–15)	25·3

	Number of specimens examined.	Wing-length mm.	Tail-length. mm.	Ratio 100 × tail / wing.	Beak-length. mm.	Ratio 100 × beak / wing
SEYCHELLES						
Mahé	6	60·0 (58–61)	39·6 (39–41)	65·0	14·6 (13·5–15)	24·4
Marianne	6	59·4 (58–61)	41·8 (40–45)	70·5	14·7 (13·5–15)	24·7
OTHER ISLANDS						
Laccadives	3	55·7 (55–57)	40·0 (39·5–41)	71·8	12·8 (12·5–13)	23·0
Pemba	16	52·8 (50–55)	35·2 (33–37)	66·7	13·7 (12·5–14)	25·9
Socotra	11	56·1 (55–57)	40·3 (38–43)	71·8	13·5 (12–14)	24·0
MASCARENES						
Mauritius *mauritiana*	8	55·1 (54–56·5)	40·2 (38·5–42)	73·0	14·0 (13–14·5)	25·4
,, *curvirostris*	7	51·6 (51–53)	32·6 (31·5–35)	63·2	16·4 (15·5–17)	31·8
Réunion *borbonica*	13	55·1 (54–58)	40·2 (38–42)	73·0	13·5 (13–14)	24·5
,, *haesitata*	19	57·7 (56–60)	40·7 (36–43)	70·5	15·6 (14–17)	27·0

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SAGITTA PLANCTONIS AND RELATED FORMS

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INTRODUCTION

The material used in the investigations recorded here was taken from the collections made by vessels of the Discovery Committee and, later, of the National Institute of Oceanography.

The bulk of these collections comes from the Southern Ocean, mainly from Antarctic waters, but a considerable quantity of material has been accumulated over the years from tropical and subtropical regions as well.

These more northerly collections while perhaps not enough to permit exhaustive studies of the life histories and distribution of single species of planktonic animals nevertheless contain much that is useful for the systematic work so necessary as a first step towards the ecological and distributional studies that might be possible when larger collections have been made in warmer seas.

This paper is an attempt to explain some anomalies of distribution of an apparently valid and homogeneous species, relatively well represented in the collections, which on careful examination appears to be a group of three forms, each, in the present state of knowledge, being entitled to specific rank.

Sagitta planctonis was described by Steinhaus (1896) from material taken in shallow net hauls off S.W. Africa. In 1905 Fowler described a new species *S. zetesios* taken by H.M.S. " Research " in deep water in the Bay of Biscay. These two species were combined into one by Ritter-Zahony in 1911 under the name *S. planctonis*. Although this arrangement has remained to the present day, it has been suggested both on anatomical grounds (Tokioka, 1939 ; George, 1952) and on distributional grounds (Moore, 1949) that two distinct forms are combined as one species.

Probably the most certain anatomical feature for specific determination of chaetognaths is the shape and position of the seminal vesicles. Unfortunately mature specimens of many species of chaetognaths are but rarely caught and *S. planctonis* is exceptionally uncommon in the fully mature state. It is for this reason that Ritter-Zahony's figure and description of the mature vesicles of this species, has of necessity been accepted by subsequent authors, despite the fact that Tokioka (1939) and George (1953) have figured *S. planctonis* with vesicles or remnants of the vesicles differently situated.

Specimens which appear to be *S. planctonis*, with seminal vesicles as described and figured by Ritter-Zahony (1911), are common in the Antarctic plankton samples of the " Discovery " Collections, and are distributed from the surface to 1500 m. Besides these, there are specimens from tropical and subtropical hauls from deep water which agree with Ritter-Zahony's table (1911, p. 30, " 90 specimens from the Atlantic Ocean "), but which have not been found with intact seminal vesicles. Traces of these structures however have been seen which appeared to be differently situated from those figured by Ritter-Zahony (1911, fig. 36). Moreover although the distribution of S. *planctonis* is well established as mesoplanktonic, specimens apparently of the same species (i.e. within the range of variation given, or implied, by Ritter-Zahony) have been taken in shallow hauls in the subtropics, associated with typically epiplanktonic forms, and often in too large numbers for this anomalous distribution to be ascribed to some freak of distribution of the mesoplankton.

Thus, from distributional evidence it seemed that there were at least two separate species in the collections grouped under one name, an opinion held for many years by Mr. J. W. S. Marr (personal communication). In the absence of any established anatomical differences this opinion remained conjectural.

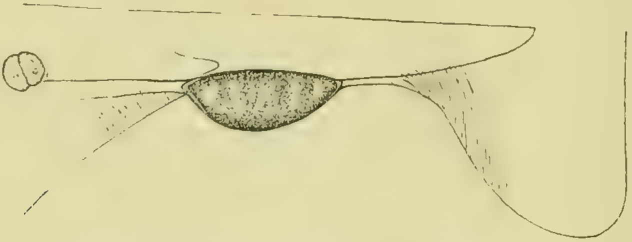

FIG. 1.—Seminal vesicle of S. *planctonis*.

Recently Mr. A. de C. Baker (also working on the " Discovery " collections) noticed, and drew my attention to, a large mature chaetognath in perfect condition (Pl. Ia) which was taken at Stn. 1685 (41° 21·8′ S., 148° 51′ E. 15.ii.36) to the East of Tasmania between 1000 and 750 m. Although the seminal vesicles (see Text-fig. 1) of this specimen were not in agreement with Ritter-Zahony's figure the specimen was in other respects identical with the subtropical forms referred to as S. *planctonis*. The Tasman sea is an area where S. *planctonis* is found in the surface waters as it is off Bermuda (Moore, 1949), S.W. Africa (Steinhaus, 1896), in the Aghulas current, off N.E. New Zealand and in parts of the North Atlantic (" Discovery " collections). I therefore supposed at first that this surface form of warmer latitudes was S. *planctonis* Steinhaus and that the specimen from Stn. 1685 was breeding in deep water as do certain other surface forms, e.g. S. *lyra* and S. *gazellae* (Ramault and Rose, 1946; Ghirardelli, 1950; David, 1955) and that the Antarctic form was the same as the cosmopolitan deep-water S. *planctonis* of Ritter-Zahony and others, and probably referable to S. *zetesios* Fowler. Examination of a number of deep living specimens from tropical and subtropical waters however, showed that while they resemble the surface form closely they are quite different from the Antarctic form.

I have therefore concluded that grouped under the one name S. *planctonis* there are three distinct species, easily distinguishable when fully mature, but closely similar in the immature stages. These are (*a*) the surface living form of tropical and subtropical waters, originally named *S. planctonis* by Steinhaus, (*b*) the deep water form also of warm latitudes named *S. zetesios* by Fowler, and (*c*) the Antarctic form described as *S. planctonis* by Ritter-Zahony, occurring from near the surface down to 1500 m. or more. I propose to return to the orignal nomenclature for the two tropical and subtropical forms, calling them (*a*) *S. planctonis* Steinhaus and (*b*) *S. zetesios* Fowler. The Antarctic form I propose to name *S. marri* after Mr. J. W. S. Marr.

SYNONYMY AND DESCRIPTION OF SPECIES

Examination of the literature shows that whereas Ritter-Zahony had recognized the Antarctic form as differing both in size at maturity and in the numbers of teeth from the " typical " deep living *planctonis*, he had not considered that any significant difference existed between *S. planctonis* Steinhaus and *S. zetesios* Fowler. This was due partly to the inadequate description of *S. planctonis* Steinhaus and partly to the absence of the species from the Gauss collections. Also, setting aside the distributional differences, the only obvious feature distinguishing *S. planctonis* from *S. zetesios* was the greater number of posterior teeth in the latter species, the Antarctic form in this respect being intermediate and apparently bridging the gap between *S. planctonis* and *S. zetesios*. It was hardly surprising that Ritter-Zahony regarded the three forms as variation (and not great variation) in one species. However the present evidence of the mature vesicles of *S. planctonis* and *S. marri* immediately separates them into two species and thus invalidates the intermediate nature of the Antarctic form *S. marri*. The difference between *S. planctonis* Steinhaus and *S. zetesios* Fowler is once again dependent upon the number of posterior teeth, and previous records show this to be consistent. Fowler (1905 and 1906) records six specimens of *S. planctonis* none of which had more than 12 posterior teeth. Michael (1911) records *S. planktonis* with up to 12 posterior teeth. Tokioka (1940) does not record more than 12 posterior teeth in specimens from the Tasman sea, and this is confirmed by Thomson (1947) from the same area, although in two size groups (see Text-fig. 2) he records up to 13 posterior teeth.

Records of *S. zetesios* are more frequent and all show a much higher maximum. For example, Fowler (1905, 1906) gives up to 19 posterior teeth, Michael (1911, 1919) up to 19, Ritter-Zahony (1911) up to 22, Burfield and Harvey (1926) up to 19, and Burfield (1930) up to 19. Some of these previous records are summarized in Text-fig. 2.

Published information on the shape and position of the seminal vesicles is conflicting. Fig. 1 in Steinhaus' paper shows no seminal vesicles despite the quite advanced ovaries. Fowler (1905) figures the vesicles of *S. zetesios* nearer the posterior fins than the tail. He shows them in the same position in the figures in the Siboga report (1906), pointing out that the seminal vesicles were only projecting slightly.

Michael (1911) shows *S. planktonis* with conical vesicles close to the tail fin, but his figure bears little resemblance to the mature vesicles of the Antarctic form, and none at all to the other forms. Ritter-Zahony (1911) figures the vesicles of the Antarctic

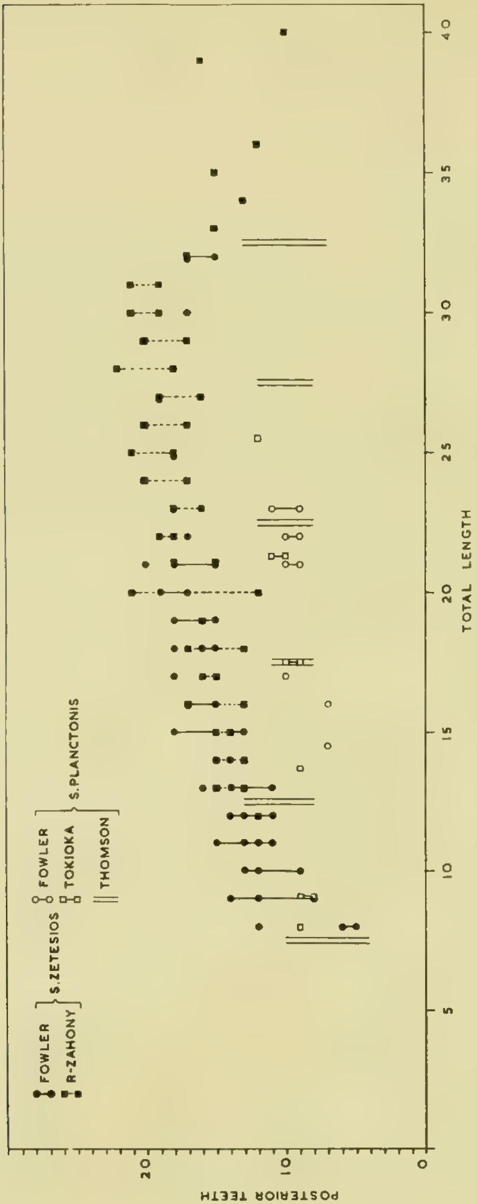

FIG. 2.—Numbers of posterior teeth plotted against body length for *S. planctonis* and *S. zetesios*. Data from previous authors.

form as conical and in contact with the caudal fin. This has been subsequently regarded as the typical *planctonis* vesicle.

The figures in Germain and Joubin (1916) are of little help ; they show *S. planctonis* with an evidently stylized vesicle in contact with both the posterior and caudal fins.

Tokioka (1939) figures the remnants of the vesicle in contact with the posterior fins—with Ritter-Zahony's figure alongside for comparison—and in his paper on the New South Wales plankton (1940) shows the rudiments of a vesicle in contact with the posterior fin.

Thomson (1947) did not figure *S. planctonis*, but in his key described the seminal vesicle as not in contact with either the posterior or caudal fins and said it " approaches the tail fin ".

Fraser (1952) said the vesicles of this species were elongated and conical near the tail fin, but his photograph shows their remnants to be near to the posterior fins.

George (1952) gives the position of the seminal vesicles as in contact with the posterior fin, but the figure given in his paper does not show any detail of the shape of the vesicles. The largest specimen recorded in his table (p. 663) is 13·0 mm., and the size range for the species given in his table of diagnostic features (opposite p. 680) is from 12–20 mm. I have not seen either *S. planctonis* or *S. zetesios* with even rudimentary vesicles at this size, nor have I seen any specimens with confluent fins as shown in his fig. 13. It is possible therefore that he is dealing with another form altogether.

S. planctonis and related forms (as a group) are easily recognized by their robust form and extensive collarette and resemble each other so closely in appearance when immature that although authors have found certain characters which did not altogether agree with Ritter-Zahony's classic description, they felt sure on other grounds of the identity of their specimens and did not attempt to distinguish them further.

Some authors have employed the name *planktonis* spelt with a " k " instead of *planctonis* with a " c " as used by Steinhaus. Although the use of " k " instead of " c " is more properly derived the first published orthography *planctonis* must stand.

Sagitta planctonis Steinhaus, 1896

(Pl. II*a*, fig. 3*a*)

Sagitta planctonis Steinhaus, O., 1896, Inaug. Diss. Kiel., pp. 1–49.
Sagitta planctonis Fowler, 1905 ; Fowler, 1906 ; Ritter-Zahony, 1909 (?) ; Tokioka, 1940 ; Thomson, 1947 ; Moore, 1949.
Sagitta planktonis Michael, 1911.

CHARACTERS :

Anterior fin rayless at the anterior end and along the inner edge : begins at the ventral ganglion. Length 24–32% of body length.

Posterior fin sharply triangular, apex of fin level with or slightly behind tail septum.

Tail stout, 19·2–21·4% of body length.

Anterior teeth up to 9, usually 6–8.

Posterior teeth up to 14, usually 10–12.

Hooks up to 11, usually 8–11.

Seminal vesicles elongate, in contact with posterior fins, simple, of the "*bedoti*" type. (see Text-fig. 1).

Ovaries completely filling body cavity when fully mature.

Collarette very prominent, extending to the tail in fully grown specimens.

Corona commences at the posterior end of the head and extends to about half way between the head and ventral ganglion. (see Tokioka 1940, fig. 86B).

Length up to 37 mm.

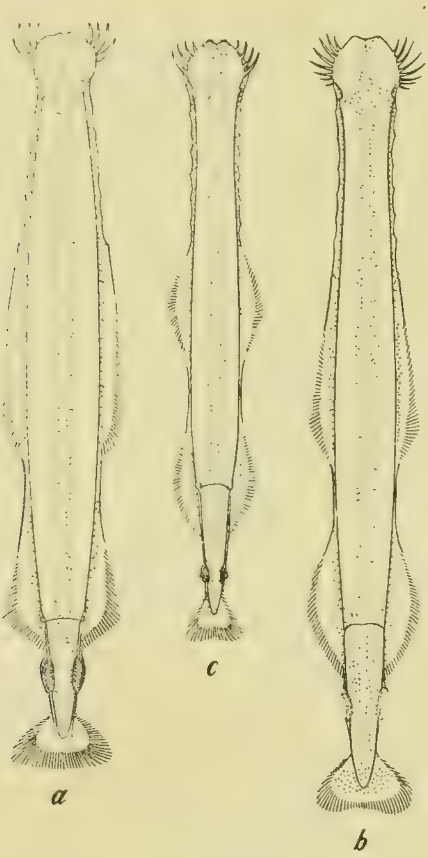

FIG. 3 — A comparison of the fin shape and position of the seminal vesicles. (a) *S. planctonis*, 37 mm. long. (b) *S. zetesios*, 38 mm. long. (c) *S. marri*, 28 mm. long.

Distribution. Bermuda, S.E. Africa, (Aghulas current area), Tasman Sea, off N.E. New Zealand, and parts of N. Atlantic. A surface living form breeding at a moderate depth (1000–750 m.).

Sagitta zetesios Fowler, 1905

(Fig. 3b)

Sagitta zetesios Fowler, G. H., 1905, Trans. Linn. Soc. Lond. (Zool.) Ser. 2 X, pp. 55–87.
Sagitta zetesios Fowler, 1906 ; Michael, 1911.
Sagitta planctonis (non Steinhaus) Ritter-Zahony, 1911 (part) ; Germain and Joubin, 1916 ; Michael, (1919) ; Burfield and Harvey, 1926 ; Burfield, 1930 (part) ; Bollman, 1934 (part) ; Kuhl, 1938 (part) ; Thiel, 1938 (part) ; Kramp, 1939 (?) ; Tokioka, 1939 ; Fraser, 1952.
Sagitta planktonis (non Steinhaus) Kramp, 1918 (?) ; George, 1952. (?)

CHARACTERS :

Anterior fin rayless or very sparsely rayed at the anterior end, beginning at or about the ventral ganglion. Length 20–26% of body length.

Posterior fin triangular, apex of fin level with tail septum.

Tail stout, 20–23% of body length.

Anterior teeth up to 12, usually 8–10.

Posterior teeth up to 22, usually 15–19.

Hooks up to 11, usually 8–10.

Seminal vesicles shape not known, but remnants of vesicle indicate that it is in contact with the posterior fin, elongate and of similar dimensions to those of *S. planctonis*.

Ovaries longest observed reached to half-way between the head and ventral ganglion.

Collarette very prominent, extending on to the tail in large specimens.

Corona similar to *S. planctonis*. See Ritter-Zahony 1911, fig. 35*a*.

Length up to 40 mm.

Distribution. A deep living form found in most deep oceans, but absent from the Antarctic.

Sagitta marri *nov. sp.* (Pl. II*b*, fig. 3*c*)

Sagitta zetesios Fowler, 1907 (*nec* Fowler 1905).
Sagitta planctonis (non Steinhaus) Ritter-Zahony, 1911 (part) ; Jameson, 1913 ; Johnston and Taylor, 1921 ; Burfield, 1930 (part) ; Bollman, 1934 (part) ; Mackinstosh, 1937 (part) ; Thiel, 1938 (part).
Sagitta planktonis (non Steinhaus) Hardy and Gunther, 1936.

Holotype a mature specimen 23·9 mm. in length taken in a 70 cm. vertical closing net which fished between 750 and 500 m., at " Discovery " station 859 : 59° 19·1′ S., 68° 51·8′ E. : 25.iv.32.

Body proportions : Total length 23·9 mm. (24·5 mm. including caudal fin) ; Tail segment 5·3 mm., 22·2% of total length ; anterior fins 3·7 mm., 15·5% of total length.

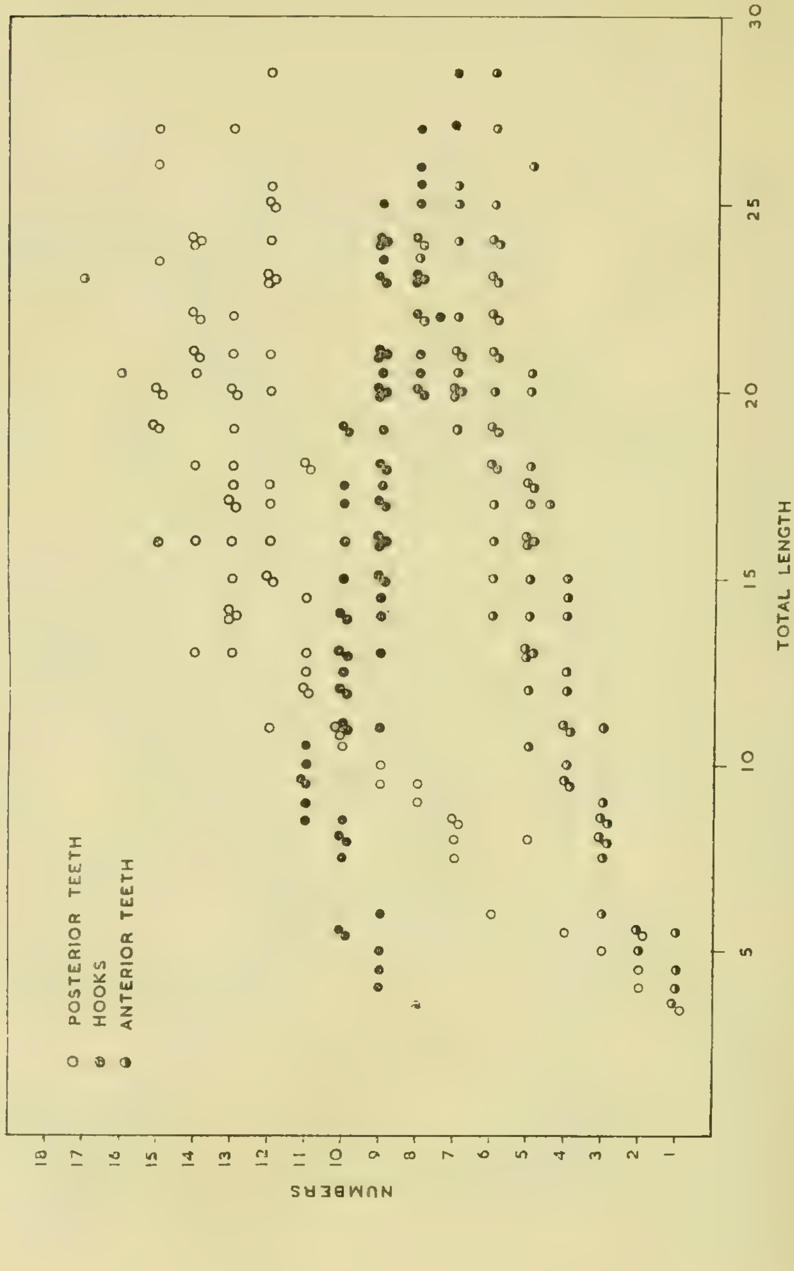

FIG. 4.—Head armature numbers plotted against body length for *S. marri.*

Head armature : Hooks 6 and 8 ; anterior teeth 6 and 7 ; posterior teeth 16 and 16.

Gonads : Ovaries 7·2 mm., 33·2% of total length ; one fully mature seminal vesicle present, the other full-sized but not full of sperms.

Paratypes : 32 specimens taken in a 1 m. closing net fished from 700–400 m. at " Discovery " station 1782 : 58° 44·6′ S.; 00° 00·7′ E.; 3.vi.36.

The range of variation given below is that of the 76 specimens shown in Text-fig. 4.

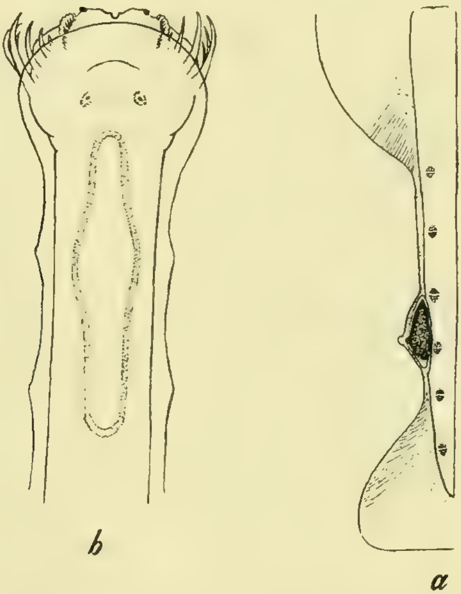

FIG. 5.—*S. marri.* (a) Shape and position of seminal vesicle. (b) Shape and position of corona.

CHARACTERS :

Anterior fin completely rayed, rounded, begins slightly behind the ventral ganglion. Length 10–19% of body length.

Posterior fin rounded.

Tail slender, 20–28% of body length.

Anterior teeth up to 8, usually 6–7 (see Text-fig. 4).

Posterior teeth up to 17, usually 14—15 (see Text-fig. 4).

Hooks 7 to 11, usually 8–9 (see Text-fig. 4).

Seminal vesicles conical, very close to tail fin (see Plate 1*b*, fig. 5*a*).

Ovaries observed up to ventral ganglion.

Collarette prominent between head and anterior fins, but very thin on remainder of the body.

Corona commences at the posterior end of the head and reaches about $\frac{1}{3}$ of the distance to the ventral ganglion (see Text-fig. 5*b*).

Length up to 28·5 mm.

Distribution Probably a purely Antarctic form, extending from the surface down to about 1,500 m., though commonest between 750 and 250 m. Breeds in deep water.

DISCUSSION

Although as already mentioned it is easy to separate *S. planctonis* Steinhaus and *S. zetesios* Fowler from *S. marri* by the shape and position of the seminal vesicles, these structures are seldom visible in the first two mentioned species (see p.437). In *S. marri* however traces of the vesicles are visible in animals as small as 12 mm. long, while no trace of a vesicle is normally visible in specimens of the other two species less than 25 mm. long. Something more is therefore needed to differentiate them when immature, and in Text-fig. 6 I have been able to show how the length of the anterior fin expressed as a percentage of the total length can be used to do so. It will be seen that this percentage is less than 20 in *S. marri*, more than 20 in *S. zetesios* and 24 or more in *S. planctonis*. As far as the two latter species are concerned however the amount of overlap is perhaps too great for this feature to be of diagnostic value except where large numbers of specimens are involved.

These percentage differences apart, the shape and structure of the anterior fins are of some taxonomic importance. In *S. marri*, as Text-fig. 3 shows, they are regularly arcuate, having their greatest width at the middle, and are completely rayed. In both *S. planctonis* and *S. zetesios* they are elongate, widest at the posterior end and either rayless or having only a few widely spaced rays in front.

Although *S. planctonis* and *S. zetesios* cannot usually be distinguished by differences in the ratio of anterior fin length to body length, the posterior teeth if plotted against the body length (Text-figs. 2 and 7) demonstrate how readily distinguishable, in their older stages at any rate, they can be. Fig. 2 has been compiled from the work of earlier authors. It includes all available previous records of *S. planctonis*, records of *S. zetesios* by Fowler (1905, 1906) and records of *S. planctonis* (= *S. zetesios*), " 90 specimens from the Atlantic Ocean " by Ritter-Zahony (1911, p. 30). Taking all sizes above 15 mm. it will be seen from this figure that only in one instance, a record by Ritter-Zahony of a specimen of *S. planctonis* (= *S. zetesios*) 20 mm. long with only 12 posterior teeth, do the two sets of data overlap. The records of Thomson (1947) for *S. planctonis*, which were given for 5 mm. size groups, have been plotted in the middle of each such size group. Text-fig. 7 has been compiled from " Discovery" data. It confirms the previous work on *S. zetesios*, apart from the one anomalous Ritter-Zahony record, and amplifies the previous work on *S. planctonis*. In this figure the data plotted were from specimens from a large number of plankton samples in the " Discovery " collections, selected so as to cover as much of the size range of the species as possible. The samples were collected at depths from the surface to 2000 m. in the North and South Atlantic Oceans, the Tasman Sea, the Indian and South Pacific Oceans at different seasons of the year. The data shown in the

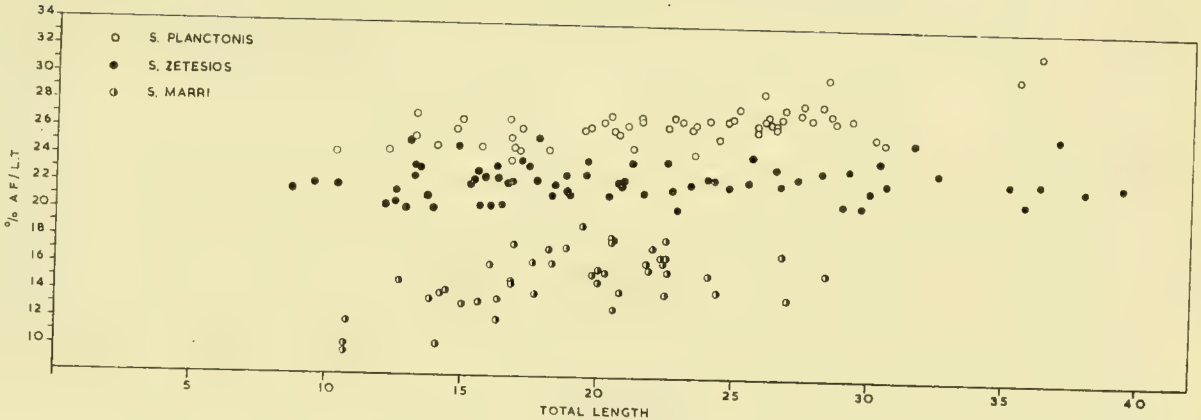

FIG. 6.—Ratio anterior fin length to body length plotted against body length.

figure can therefore be taken to cover seasonal and distributional variations, if any, though the sample is not a fair one for statistical purposes.

It is evident then that above 15 mm. specimens of *S. planctonis* and *S. zetesios* can readily be distinguished by their posterior teeth numbers and that below this size these numbers more or less overlap and would not be a reliable distinguishing feature. I have been unable to find a method of distinguishing them below this size, and the small specimens in Text-figs. 2 and 7 have been identified only by being present in hauls which apparently contained but one species. This is not altogether satisfactory and it is hoped that further work may produce a reliable method of identifying the young forms.

Distributional evidence shows that *S. zetesios* is a typically mesoplanctonic form, while records of *S. planctonis*, although scarce, all point to its being epiplanktonic. The species described by Moore (1949) from the surface waters round Bermuda is almost certainly *S. planctonis* although he gives no counts of posterior teeth to confirm it. Steinhaus's records were from shallow hauls as also were those of Tokioka (1940). Thomson (1947) gives the vertical distribution as abundant between 0 and 100 m., and numerous down to 500 m. *S. planctonis* has been taken in shallow hauls at various "Discovery" stations e.g. **1608**.—36° 07′ S., 22° 53·8′ E., 10.xi.35. **1609**.—37° 08·4′ S., 27° 03·1′ E., 11.xi.35. **1610**.—38° 31·9′ S., 31° 11·5′ E., 12.xi.35. **2729**.—35° 37′ S., 160° 22′ E., 21–22.x.50. **2730**.—35° 58′ S., 163° 39′ E., 22.x.50. **2734**.—45° 00′ S., 173° 39′ W., 5–6.xi.50. **2920**.—48° 45′ N., 18° 52′ W., 4.vi.52.

KEY

S. planctonis group

Robust chaetognaths, usually opaque and white when preserved, having an extensive collarette which in well preserved specimens extends to the tail, and in all specimens to the anterior fins.

1.	Length of anterior fin more than 20% of total body length	2
	Length of anterior fin less than 20% of total body length	*S. marri*
2.	Posterior teeth usually more than 14*, deep water form	*S. zetesios*
	Posterior teeth usually less than 14*, shallow water form . . .	*S. planctonis*

* See Text-fig. 7.

ACKNOWLEDGMENTS

I would like to thank Mr. J. W. S. Marr for a great deal of advice and assistance, and Dr. J. H. Fraser, F.R.S.E. for reading the typescript.

SUMMARY

Specific distinction between *S. planctonis* and *S. zetesios*, on the one hand, and *S. marri*, on the other, depends primarily on the shape and position of the seminal vesicles; three other features, the shape of the fins, the length of the anterior fins, and the total length at maturity provide additional diagnostic characters. By the use of these points *S. marri* can be distinguished at all sizes above about 8 mm.

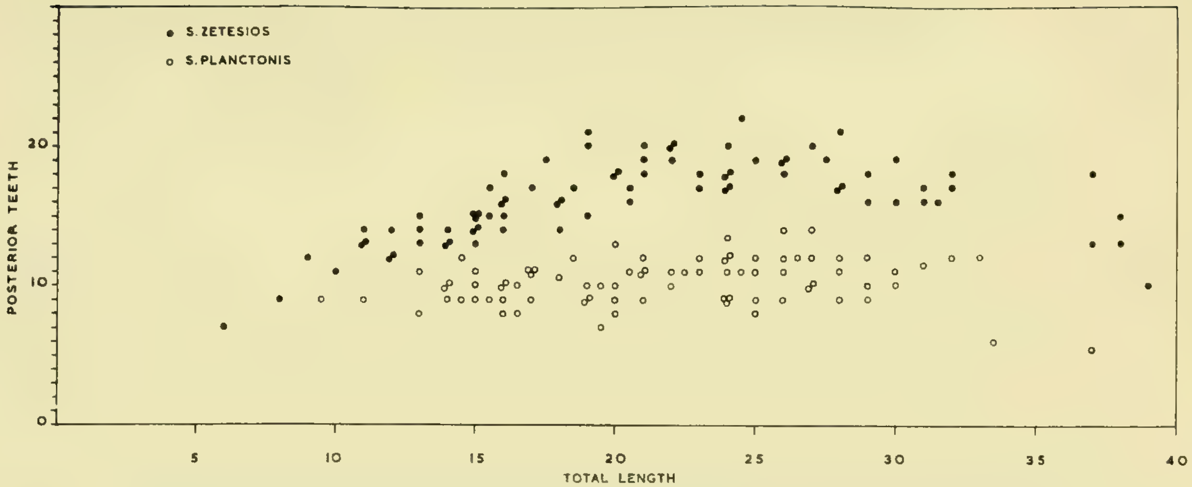

FIG. 7.—The mean of the sum of each pair of posterior teeth plotted against body length for *S. planctonis* and *S. zetesios*. Data from "Discovery" collections, from many stations in different localities at different seasons.

The separation of *S. planctonis* and *S. zetesios* is less satisfactory and rests upon the numbers of posterior teeth in animals over 15 mm. in length which is the only observed taxonomic difference. It is probable that depth distribution will provide further supporting evidence for the existence of these two undoubtedly separate species, but this has yet to be fully worked out.

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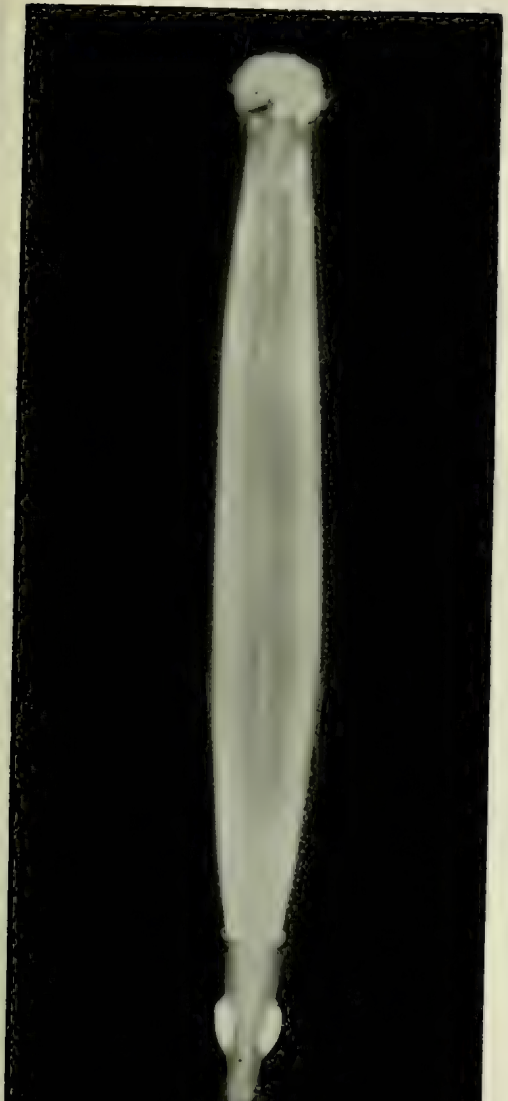
PLATE 11

(a) *Sagitta planctonis* Steinhaus. A fully mature specimen 37 mm. long.

(b) *Sagitta marri* nov. sp. A mature specimen 28 mm. long.



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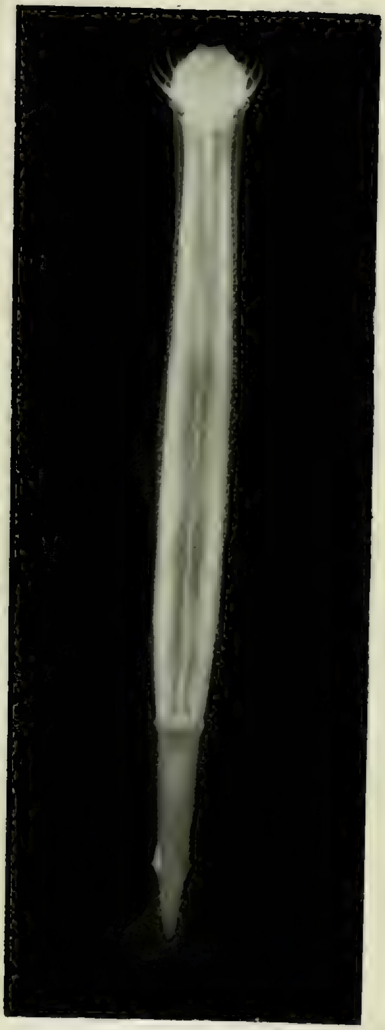

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EVOLUTIONARY TRENDS IN THE CLASSIFICATION OF CAPITATE HYDROIDS AND MEDUSAE

PRESENTED
24 JAN 1957

W. J. REES

BULLETIN OF
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ZOOLOGY Vol. 4 No. 9
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EVOLUTIONARY TRENDS IN THE CLASSIFICATION OF CAPITATE HYDROIDS AND MEDUSAE

By WILLIAM J. REES, D.Sc.

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SYNOPSIS

The concept now outlined of evolutionary trends in Capitate hydroids departs considerably from the traditional ideas of evolution in gymnoblastic hydroids, and is based on a consideration of the species as a whole. The hydroids and their medusae are demonstrated to form mosaic patterns from which it is possible to create a single integrated classification to reflect relationships, and to replace the old dual system of unrelated separate systems.

No attempt has hitherto been made along these lines to consider the evolution of basic features and the relation of form to function in hydroids and their medusae. Here the significance of evolution in the hydranth, the development of a firm perisarc, the positioning of the gonophores and the gonophore itself are discussed in relation to the main trends in the group. The lower Corymorphines are demonstrated to be essentially primitive and from them are derived the Tubularoids, the *Acaulis-Myriothela* line and all the colonial Corynoidea.

In the outline classification which follows, four superfamilies are created, the Tubularoidea, the Tricyclusoidea, the Acauloidea and the Corynoidea to denote well marked groups and evolutionary trends in the Capitata. Other changes include the recognition of the subfamilies Euphysinae, Boreohydrinae, Monocoryninae, Myriothelinae and the creation of the Hydrocorynidae for *Hydrocoryne miurensis*.

1. INTRODUCTION

> " It will assuredly seem strange that those principles of classification which have been acknowledged as the only sound ones, and which have been our guide in the study of every other group of the animal kingdom, should be almost entirely ignored in our attempts at a systematic arrangement of the Hydroida."
>
> G. J. Allman, *Ann. Mag. Nat. Hist.* (3) vol. XIII, p. 345, 1864.

THE study of hydroids and their medusae gained great impetus about one hundred years ago with the classical researches of Michael Sars, Edward Forbes, Thomas Strethill Wright, Thomas Hincks, George James Allman and Philip Henry Gosse. These early field naturalists were fully aware of the need for extending the knowledge of the life history of these animals and considerable progress was made in linking up hydroids with their medusae, either by rearing young hydroids from medusae or in obtaining newly liberated medusae from hydroids. Even ninety years ago the dual system of classification—one for hydroids and the other for their planktonic medusae—was beginning to bedevil the classification of this group, and, although the relationship of a particular hydroid to a particular medusa might become known beyond doubt, the practice of using two entirely different names for different phases of the same species continued.

The opening words of Allman's pioneer efforts (1864) to achieve a sound basis for classification deplores this practice and goes on in another paragraph :

" Yet this is totally at variance with the first principles of natural classification and of a scientific nomenclature ; and the sooner we get rid of it the better for the harmony of biological method, and the progress of that department of zoology in which it has prevailed."

It is obvious that Allman had a clearer grasp of first principles in the classification of hydroids and medusae than any of his contemporaries and his statement that " An adequate conception of the Hydroid can thus only be obtained by regarding it as the product of two factors, one of them finding its expression in the trophosome, and the other in the gonosome " was so far ahead of his time that even today we find few authors have caught up with this principle.[1]

In capitate hydroids and medusae the need for maintaining a dual classification has almost disappeared although there are still gaps to be filled. A single classification for both hydroids and medusae of this group is now possible but to evolve a natural classification is much more difficult. The latter is basically an assessment of the true value of the various characters used in classification, that is, we must consider the mosaic to appreciate where a species stands in relation to others.

In recent years two papers have been written on interrelationships in gymnoblastic hydroids on the conventional lines of dealing with only one phase in the life history and without considering form in relation to function. Fraser's attempt (1943) need not be seriously considered (Text-fig. 1), but a very interesting paper on the origin of the hydroid family Corymorphidae appeared from the pen of P. L.

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[1] We find that Fraser (1944) for instance, seldom gave any adequate description even of the newly liberated medusae of the medusa-bearing species while some of his ideas on classification were almost pre-Hincks in concept.

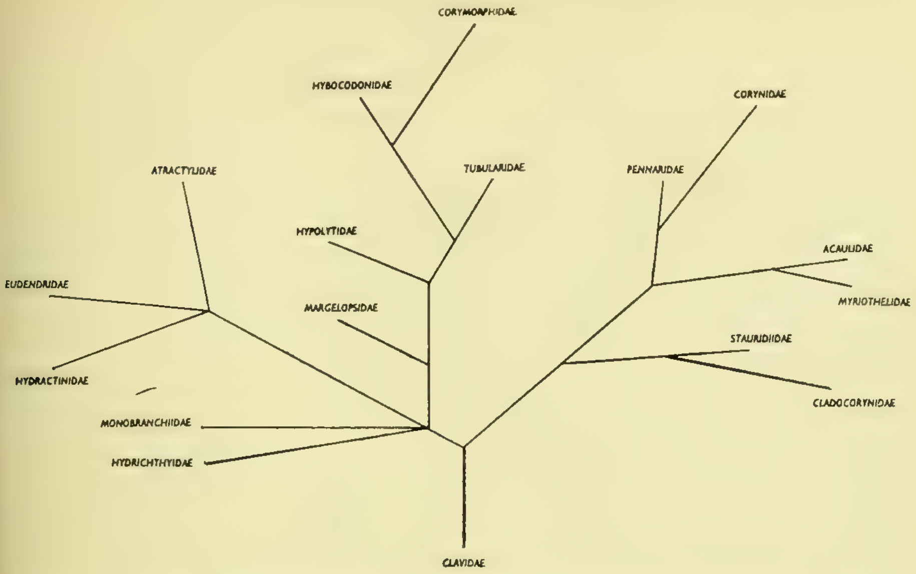
CORYMORPHIDAE
HYBOCODONIDAE
CORYNIDAE
ATRACTYLIDAE
TUBULARIDAE
PENNARIDAE
HYPOLYTIDAE
ACAULIDAE
EUDENDRIDAE
MARGELOPSIDAE
MYRIOTHELIDAE
STAURIDIIDAE
HYDRACTINIDAE
CLADOCORYNIDAE
MONOBRANCHIIDAE
HYDRICHTHYIDAE
CLAVIDAE

FIG. 1. Phylogeny in North American gymnoblastic hydroids as envisaged by Fraser (1943).

Kramp in 1949. In it he set forth his views on interrelationships in hydroids of the Corymorphidae, the Tubulariidae, Corynidae and related families. He followed Kühn (1913) in the view that the Corynidae are the most primitive (Text-fig. 2) and from which all other capitate forms are derived. He traced two separate lines of evolution called the *Tubularia*-line, and the *Corymorpha*-line, culminating in the Tubulariidae and Corymorphidae respectively.

This theory appeared plausible from the conventional approach, but years of experience on living hydroids and medusae at Plymouth and elsewhere had already inclined me to the belief that the less specialized Corymorphine hydroids were more primitive in all essentials than other capitate forms. The appearance of Dr. Kramp's paper renewed my interest in this question and although I could not accept the view that most of the solitary forms were derived from the colonial Corynidae, it was soon evident to me that any alternative theory on conventional lines would not solve the problem of relationship.

This led me to what I am inclined to call basic principles in the classification of hydroids and medusae in order to try to assess the evolutionary significance of the various features on which classifications are based. In attempting to establish basic principles from which to work, I am very conscious that some of them are possibly axiomatic in other fields of zoology and probably by no means new, but in the study of the Hydrozoa there has been remarkably little consideration given to fundamental questions of relating form to function and the probable evolution resulting from it.

In this paper it is not possible to present more than an outline of the Capitata

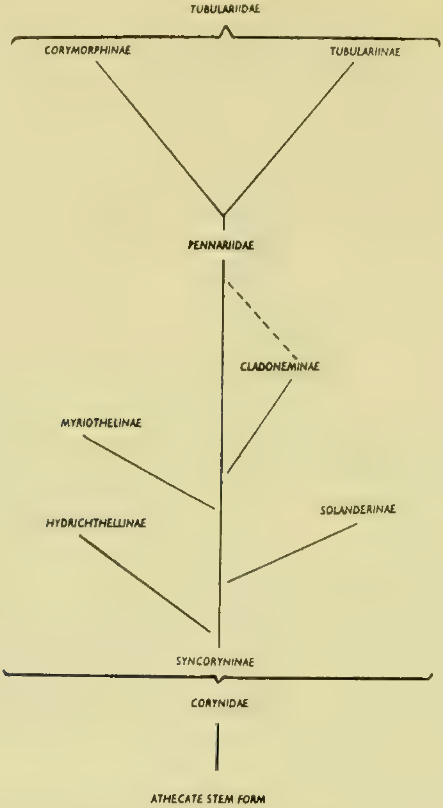
TUBULARIIDAE
CORYMORPHINAE
TUBULARIINAE
PENNARIIDAE
CLADONEMINAE
MYRIOTHELINAE
SOLANDERINAE
HYDRICHTHELLINAE
SYNCORYNINAE
CORYNIDAE
ATHECATE STEM FORM

FIG. 2. Phylogeny in gymnoblastic hydroids according to Kühn (redrawn from Kühn, 1913).

and the way I think they have evolved, a concept which departs considerably from the traditional ideas of evolution in gymnoblastic hydroids. In order to make the paper intelligible to the general zoologist and the student, some of the facts have been repeated in the sections on mosaic patterns and relationships in order to clarify the general picture, and there are more illustrations than would be needed by the few specialists familiar with this group.

During the last twenty years I have gained much from earlier authors, and over such a period it is impossible now to be sure that I have acknowledged in the bibliography all whose ideas have influenced the development of this paper. It was not until 1950–51 that the ideas for its completion began to take shape, and although I explored other avenues, none, however, yielded so satisfactory an overall pattern of Capitate evolution as outlined here.

It is to the late Edward T. Browne that I owe the opportunity to begin the study of this group at Plymouth from 1936 to 1940, the ultimate aim of which he envisaged as a single classification of hydroids and their medusae. I also wish to acknowledge with gratitude the encouragement I received from the late Edgar J. Allen, C.B.E., F.R.S., the late Stanley W. Kemp, F.R.S., and Dr. F. S. Russell, C.B.E., F.R.S., during the time I was a member of the scientific staff of the Plymouth Laboratory.

This paper could not have been written, however, without the many facilities granted to me at the British Museum (Natural History), and, in particular, I wish to thank Sir Gavin de Beer, F.R.S., for much encouragement. I am very grateful to Professor Hjalmar Broch for many stimulating discussions in Oslo, in September, 1955, but I do not wish to imply that he is in agreement with all or any part of this paper. I also wish to thank Dr. Marta Vannucci for reading the manuscript and for suggesting the inclusion of Figure 58 and my colleague Mr. Ernest White for much assistance in the preparation of the report. Other acknowledgments are given in the text.

2. EVOLUTION IN THE POLYP AND DIVISION OF LABOUR

(a) *Evolution in the polyp*

Sessile colonial invertebrates are generally considered to have arisen from free swimming solitary individuals which have adopted a sedentary habit and have later become colonial animals. This natural outcome of the adoption of a sedentary habit is an axiomatic principle which applies also to the Hydrozoa and it is therefore surprising that Kramp (1949) suggests that the solitary Corymorphidae are derived from colonial forms like *Asyncoryne* (Text-fig. 3). This is quite unlikely to have

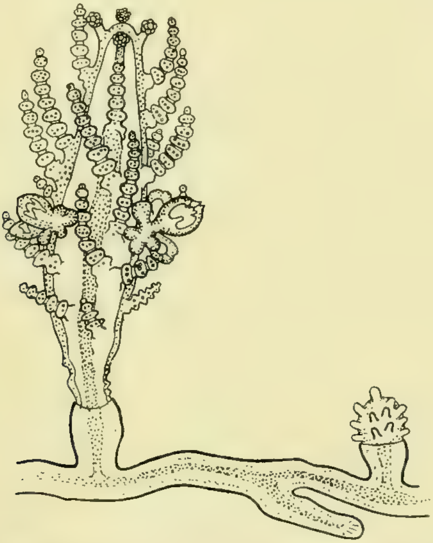

FIG. 3. *Asyncoryne ryniensis* Warren, a colonial hydroid with scattered moniliform body tentacles and an oral whorl of short capitate tentacles (redrawn from Warren, 1908).

taken place, a view already expressed by Totton (1954) "from general considerations".

We must therefore regard the solitary hydroid as being nearer the ancestral type, and, in considering capitate hydroids we have solitary forms in the Corymorphidae, the Tubulariidae, the Tricyclusidae, the Margelopsidae, the Acaulidae and the Myriothelidae, all the other families including the Corynidae being colonial.

As will be noted (p. 504) the hydromedusae are now generally believed to have either an actinuloid ancestor or to have descended from medusae having an actinuloid stage in their life history[1]; these views are elaborated on pp. 503–506.

The actinula persists chiefly in the solitary hydroids and in its development the aboral whorl develops first, these tentacles corresponding to the medusa tentacles in Trachymedusae with a direct development. The oral whorl appears late in the development and is peculiar to the Hydroida.

I know of no primitive anthomedusan hydroid in which only the aboral whorl is present, all modern species having an oral whorl in addition. Two whorls of tentacles are found in the Corymorphidae, the Tubulariidae and the Margelopsidae and we can regard the Tricyclusidae, the Acaulidae and the Myriothelidae as more advanced because they have secondary whorls developed in the budding area between these primary whorls. We see the retention of this basic pattern of two whorls in some colonial forms, e.g., in one species of *Dipurena* and in *Cladonema radiatum*; they are also the first whorls to appear in the developing polyps of *Halocordyle* (*Pennaria*) and *Stauridiosarsia*.

In the three families with this basic tentacle arrangement (the Corymorphidae, the Tubulariidae and the Margelopsidae) the simplest kind of hydranth is found in the lower Corymorphines. In these forms there is no diaphragm in the hydranth and there are no stem canals or any of the elaborate features associated with the specialization we find in *Corymorpha nutans* and the Tubularians (see p. 499).

Examples of the modern survivors of this early Corymorphine condition are *Hypolytus peregrinus* Murbach, *H. obvoluta* Kramp and *Euphysa aurata* Forbes. In the first two both whorls are moniliform, that is, the nematocyst batteries are grouped like so many beads on a string, which allows the tentacle to be highly contractile.

The moniliform condition exists also in the medusae of *Euphysa* and *Corymorpha* and also in a degenerate condition in those of a great many species of medusae (but see p. 492 for details of these) and I am inclined to regard this type of moniliform tentacle as very primitive and inherited unchanged from a medusoid ancestor. Even in the hydroids *Hypolytus peregrinus* (Text-fig. 4) and *H. obvoluta*, the oral tentacles are much shorter than the aboral ones and this condition leads on to the short capitate tentacle retaining only a single knob as in the hydroid *Euphysa aurata* (Text-fig. 5).

This is probably the way in which the short capitate tentacle originated and this type of tentacle is characteristic of the oral whorl occurring either in the larval or adult hydroid of the Corymorphidae, the Tubulariidae, the Margelopsidae, the

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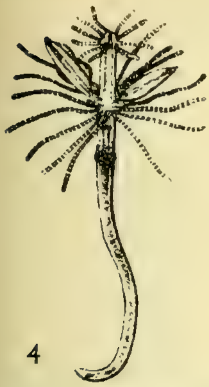
[1] Here I have not considered remoter ancestors, so that the theories of Hadzi (1944) and Jägersten (1955) concerning bilaterally symmetrical metazoan ancestors lie outside the scope of this paper.



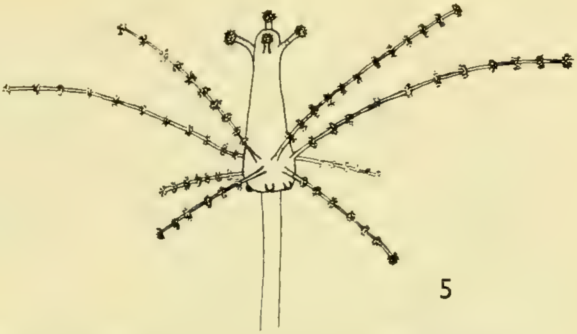


FIG. 4. *Hypolytus peregrinus* Murbach, a solitary Corymorphine with moniliform tentacles in both oral and aboral whorls (after Murbach, 1899).

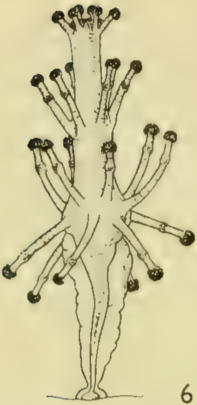
FIG. 5. *Euphysa aurata* Forbes, a solitary Corymorphine in which the oral whorl is capitate and the aboral whorl is moniliform ; hydranth of a young polyp. with tentacles fully extended (after Rees, 1937)

Tricyclusidae, the Acaulidae, the Myriothelidae and in all the colonial capitate hydroids. As a basic type of tentacle it becomes duplicated on the body of the hydranth in the inter-whorl area in a large number of families.

To return to the moniliform tentacle it appears that the aboral tentacles of *Euphysa* and *Hypolytus* hydroids have been retained in their primitive form only because the feeding habits of the hydroids favour the retention of the very long extensile fishing tentacle of the medusa. In these hydroids the tentacles are extended radially over the soft mud to trap any organism creeping over them. With the adoption of firmer substrata, the tentacles lost their need to be very extensile, this permitting a scattering of nematocyst armature and the evolution of a stouter, more rigid, and less contractile tentacle. This, the filiform type, is the aboral tentacle we have in *Corymorpha nutans*, the Tubularians, the Halocordylidae (Pennariidae) and the Acaulidae, and in vestigial form in the Corynidae.

The moniliform arrangement still persists in aberrant survivals like the colonial hydroid *Asyncoryne ryniensis* Warren (Text-fig. 3) in which the aboral moniliform tentacles have become scattered over the body of the hydranth perhaps as a result of the lengthening of the body of the hydranth itself. In the solitary hydroid, *Tricyclusa singularis*, they persist only in a very imperfect form (Text-fig. 6). Both these forms could have arisen along independent lines from an *Euphysa*-like ancestor (see p. 514).

Euphysa thus represents, as regards the hydranth, a basic type from which several evolutionary lines can be traced. The higher Corymorphines (like *Corymorpha nutans*), the Margelopsidae and the Tubulariidae, although not arising directly from an Euphysid could be derived from a descendant through partial disappearance of the nematocyst battery on the oral tentacles and the evolution



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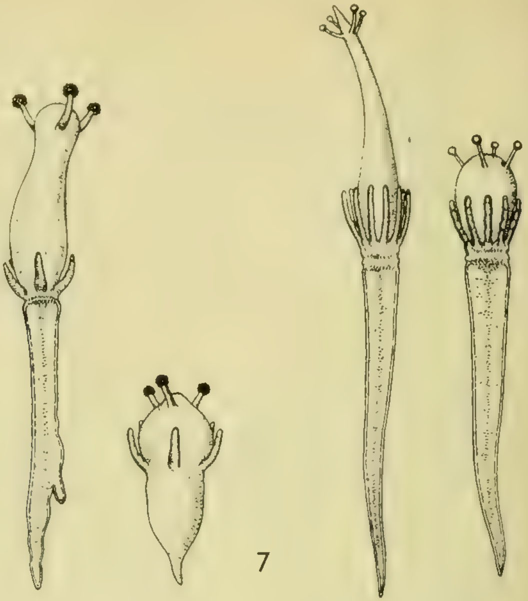

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FIG. 6. *Tricyclusa singularis* (Schulze), an aberrant solitary capitate hydroid in which the moniliform arrangement of nematocysts persists in an imperfect form (redrawn after Vervoort, 1947).

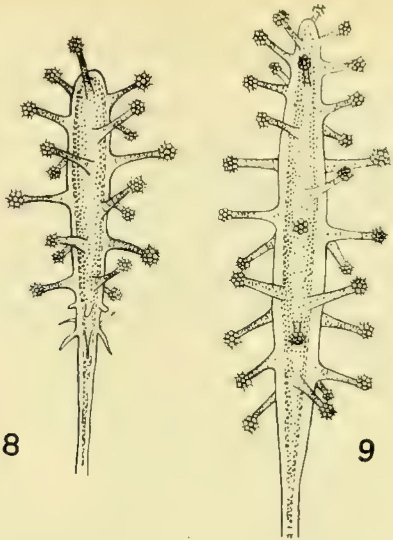
FIG. 7. *Corymorpha nutans* M. Sars: planktonic larval polyps with capitate oral tentacles and filiform aboral ones (after Hartlaub, 1907).

of filiform tentacles in the aboral whorl. There are also secondary changes due to elaboration, size, and the influence of habitat that need not concern us at this point.

This intermediate Corymorphine may have been something like the larval *Corymorpha nutans* with its capitate oral tentacles, its filiform aboral tentacles and the absence of a diaphragm (Text-fig. 7). Such a form could be envisaged as an unspecialized ancestor which could be the starting point for other evolutionary lines, viz. :—elaboration of the solitary form culminating in *Myriothela*, and also in the development of a colonial habit as in *Coryne*.

If we consider only the hydroid of *Cladonema* (leaving its highly evolved medusa out of consideration) we have here in the form of the polyp (Pl. 12, fig. 1) the simplest type of colonial hydroid from which the colonial Corynoidea (except the Asyncorynidae and the Cladocorynidae) are evolved (see p. 514).

It has not been generally realized that in some Corynidae, the primary hydranths of a colony regenerating after a period of dormancy are different from later secondary or tertiary hydranths. In *Staurocoryne filiformis* the first polyp has well developed filiform tentacles, but secondary ones have vestigial ones and they may disappear completely in tertiary polyps (Text-figs. 8 and 9). Hartlaub (1895), to judge from his figures, seems to have encountered the same phenomenon in *Stauridiosarsia*



FIGS. 8 and 9. *Staurocoryne filiformis* Rees: (8), primary polyp from a regenerating stolon (after Rees, 1936); (9), fully developed hydranth of three months old colony (original). Note the disappearance of the filiform tentacles.

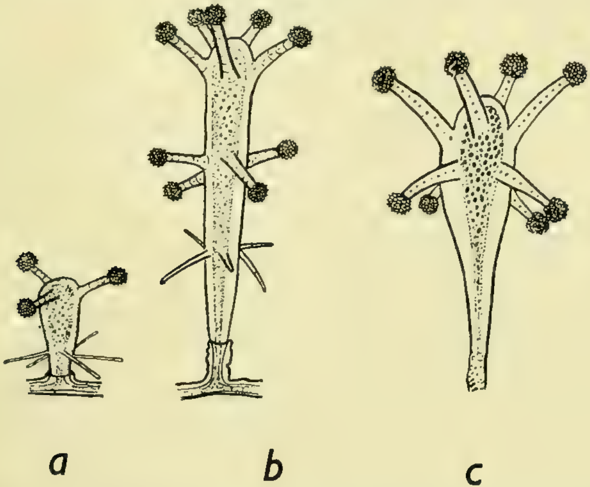


FIG. 10. *Stauridiosarsia producta* (Wright): *a–c*, loss of filiform tentacles; *a*, developing polyp with two primary whorls; *b*, fully developed polyp with filiform tentacles (both after Rees, 1938); c, polyp without filiform tentacles (redrawn after Hartlaub, 1895).

producta (Text-fig. 10, *a–c*) and these changes may represent the general trend towards the loss of the filiform tentacles in the Corynidae.

At one time a miscellaneous assemblage of corynids, corymorphines and tubularians were grouped together either with *Halocordyle* (*Pennaria*) in the Halocordylidae or with *Cladonema* in the " Stauridiidae " because of the possession of these filiform tentacles (in association with an oral whorl of capitate tentacles), but this kind of arrangement persists only in out-of-date classifications like those of Fraser (1944).

From the basic type of Corynoid hydranth the typical Corynid has been evolved by the addition of whorls of short capitate tentacles ; these are in whorls in some primary polyps, becoming scattered in later polyps. Side by side with this development the filiform or " false " tentacles tend to disappear.

Sometimes the filiform tentacles disappear completely leaving only an oral whorl of capitate tentacles as in *Hydrocoryne miurensis* and *Cladonema myersi* (Text-fig. 11).

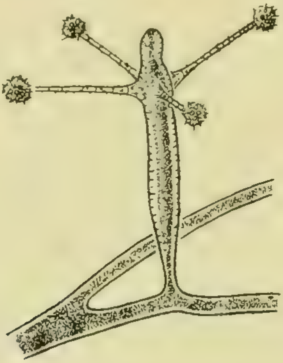


FIG. 11. *Cladonema myersi* Rees : the filiform tentacles have disappeared in this species of *Cladonema* leaving only the oral capitate whorl (after Rees, 1950).

The early naturalists regarded the higher Corymorphines and the Tubularians as the highest evolved and most elaborate of the gymnoblastic hydroids. This is true in so far as we can regard them as representing the greatest elaboration of the solitary hydroid and the metabolic activity of a large polyp must approach that in many a well developed colonial form (Text-fig. 12). The most noticeable feature is the large size of these large polyps (*Corymorpha nutans* goes up to 11·4 cm. in length and *Branchiocerianthus imperator* up to 224 cm.). This implies, and there are, structural modifications which accompany gigantism, for example, the special cushion ring (diaphragm) of parenchyma at the base of the aboral whorl of tentacles, the parenchyma and canals in the stem, the very large number of rooting filaments, the large number of tentacles and the increase in the budding zone by the expansion of this area into long, hollow, branching blastostyles. *Branchiocerianthus*, itself, with its bilateral symmetry may be further modified for feeding in a current.

The solitary polyps of the Acauloidea (see p. 515) proceeded along a different line from the erect Tubularoids, and the failure to develop a proper hydrocaulus (as will be noted on p. 466) may be associated with the feeding habits of the myrio-

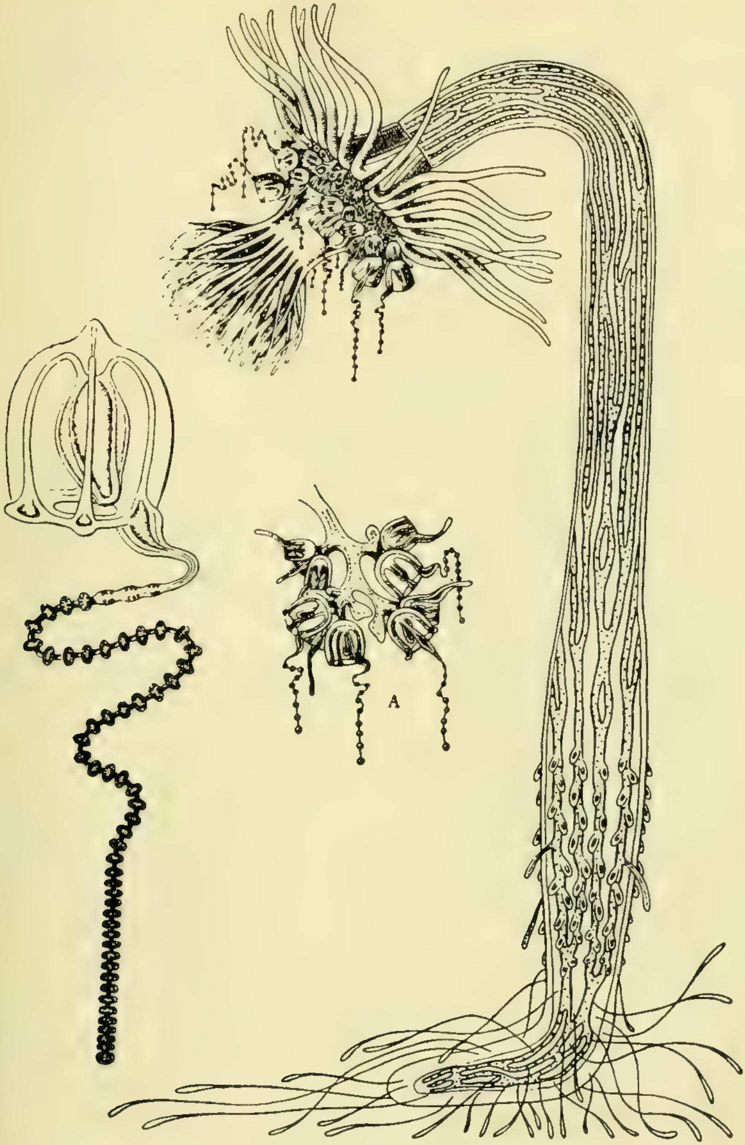


FIG. 12. *Corymorpha nutans* M. Sars, an elaborate solitary hydroid (after Allman, 1872).

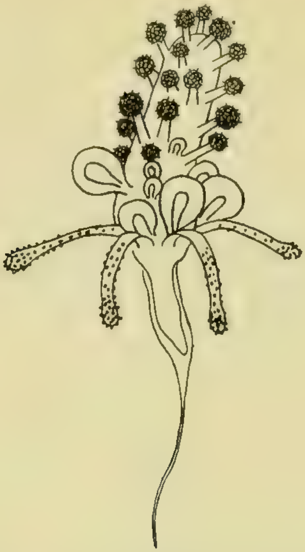
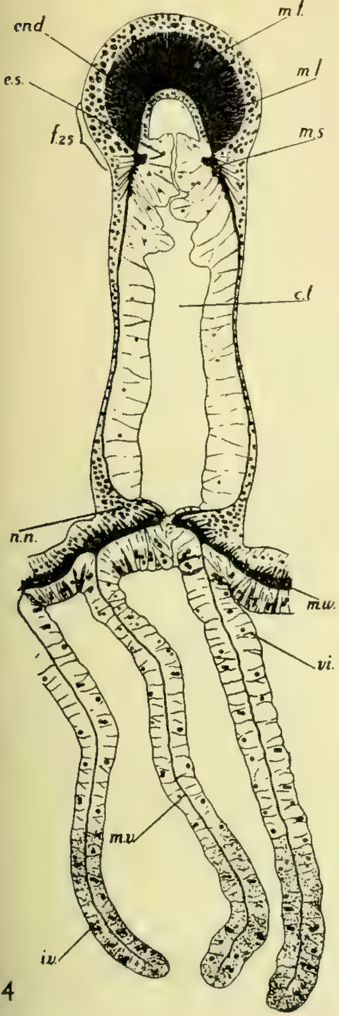


FIG. 13. *Acaulis primarius* Stimpson: young polyp with male gonophores (redrawn after Hyman, 1940). Note the gelatinous tube and anchoring filaments as in *Euphysa*, and the multiplication of short capitate tentacles in the intertentacular area.

theline polyp. *Acaulis* is but little removed from the mud-dwelling, primitive Corymorphine but the tendency to become vermiform is already apparent in the lengthening of the hydranth and the multiplication of capitate tentacles in the intertentacular area (Text-fig. 13). This tendency to elongate the polyp and consequent enormous multiplication of the number of short capitate tentacles on the body of the hydranth culminates in the highly specialized myriothelines where there are single polyps up to 30 cm. in length (*Myriothela austrogeorgiae* Jäderholm, 1905). Associated with this elaboration is an increase in the endodermal absorptive surfaces by the development of endodermal villi (Text-fig. 14). The fixed gonophores are borne on the body of the hydranth in some species, while in others special coryniform tentacles are developed and these are transformed into blastostyles (Text-fig. 15).

Great importance was attached to the presence of the supporting lamella in *Coryne* and tubularoid hydroids by Kramp (1949) who regarded continuity of the mesogloeal lamella, separating the endoderm of the hydranth from that of the tentacle as a primitive feature. It seems to have influenced him in developing his theory of a *Tubularia* line and a *Corymorpha* line in the Capitata.

It has not been possible to follow up this idea concerning the supporting lamella as fully as could be wished in this paper. The hydroid *Euphysa aurata* has however been thoroughly examined from excellent serial sections kindly given to me by Dr. Jöran Hult in 1939. There is no doubt that the lamella is continuous, separating



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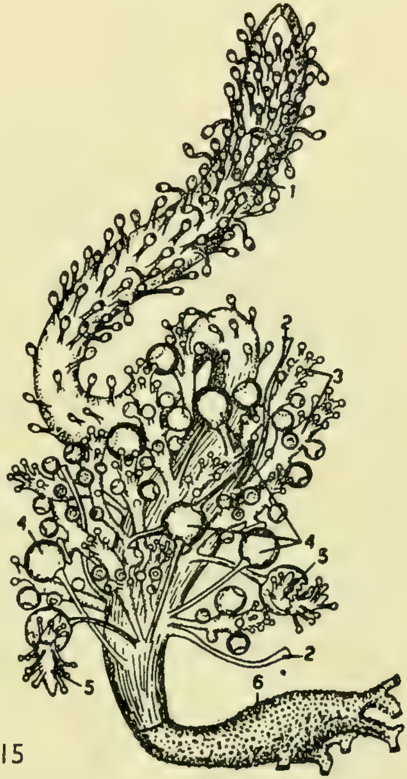

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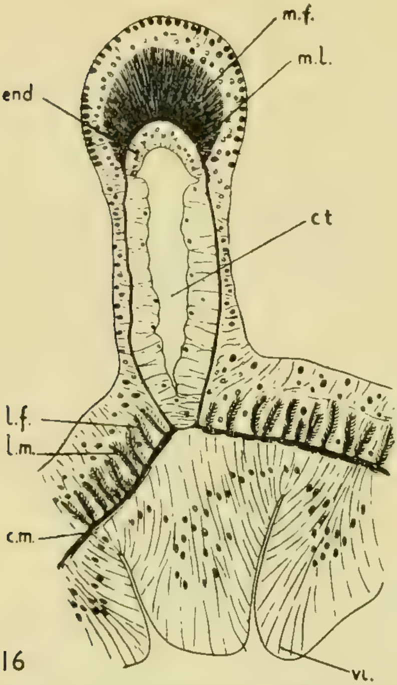
FIG. 14. *Myriothela penola* Manton: transverse section of hydranth body, showing endodermal villus (after Manton, 1940).

FIG. 15. *Arum cocksi* Vigurs, an elaborate Myriotheline hydroid (after Allman from Hyman, 1940): (1), anterior portion with capitate body tentacles; (2), clasper; (3), coryniform blastostyles; (4), ripe eggs held by claspers; (5), actinula being released; (6), perisarc-covered stem with modified anchoring filaments.

off the endoderm of the capitate tentacles in the oral whorl, but in the aboral moniliform whorl the lamella is interrupted (or as Kramp states, the supporting lamella



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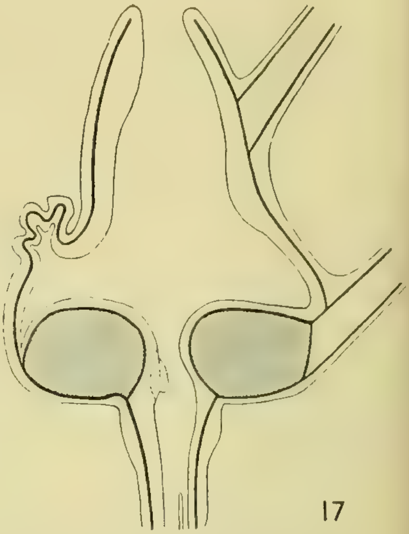

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FIG. 16. *Myriothela capensis* Manton : diagrammatic transverse section of a body tentacle and body wall to show the continuous mesogloea across the base of the tentacle ; *c.t.*, endodermal cavity of tentacle ; *c.m.*, circular muscle process ; *end.*, endoderm ; *l.f.*, longitudinal mesogloea flanges projecting into ectoderm ; *l.m.*, longitudinal muscles inserted on to mesogloea fibrils ; *m.f.*, apical pad of mesogloea fibrils ; *m.l.*, basal layer of solid mesogloea ; *vi.*, endodermal villus (after Manton, 1940).

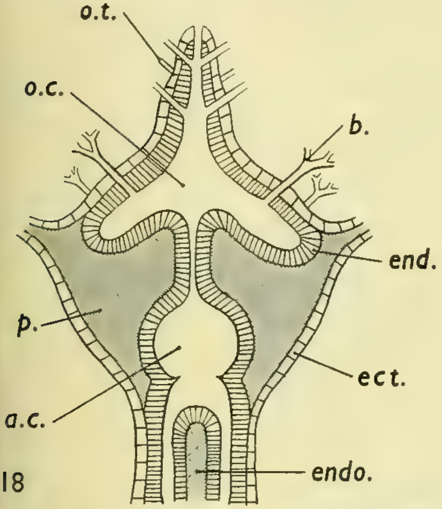
FIG. 17. Diagrammatic representation of the hydranth of *Tubularia* in longitudinal section showing the parenchymatous cushion (shaded) and the mesogloeal lamella (heavy black line) (redrawn from Grönberg, 1898).

is absent). Manton (1940) gave an excellent figure of the continuous lamella in the short capitate tentacle in *Myriothela capensis* (Text-fig. 16) and Kramp stated that the same condition prevails in the typical Corynids where the tentacles are also all short capitate ones.

It is possible to hold the view that the lamella continues intact across the base of the tentacle, only when that tentacle is a small structure, and we must remember that the short capitate tentacle develops without much local disturbance of tissue. There is, however, considerable local disturbance of the body wall during the formation of the larger aboral tentacles and the lamella may never be repaired subsequent to the formation of this type of tentacle. In other words, the presence or absence of a supporting lamella may bear a direct relation to the size of the tentacle developed.

In *Tubularia*, Grönberg (1897, pl. 4, fig. 1) has shown that the lamella, associated with the parenchymatous cushion, cuts off the endoderm of the tentacles (Text-fig. 17), but this seems to be a secondary development associated with the form of the cushion in *Tubularia* and may not be a primary feature as believed by Kramp. Enough has been said to indicate that the supporting lamella may be found to have little significance in classification when it is investigated more fully.

In the higher Corymorphines (such as *Corymorpha nutans*) there is a gastric diaphragm which divides the cavity of the hydranth into an oral and an aboral chamber (Text-fig. 18) and the stem of the hydranth is filled with parenchyma except for a series of peripheral canals representing the original cavity (Text-fig. 19). Primitive Corymorphines of small size do not possess this diaphragm which is also found in a modified form in *Tubularia*. This diaphragm is of great interest to students of phylogeny in Siphonophores but as regards the Corymorphines and Tubularians its origin seems to me to be linked with the large size reached in the polyp of these forms. Although it later acquired a more specialized function it must have originated as a thickening of the hydranth wall to support a large whorl of tentacles and the same cause (i.e., a large hydranth head) necessitated a stiffening of the polyp stem resulting in the so-called " endocord " of Garstang (1946, p. 124, fig. 18).



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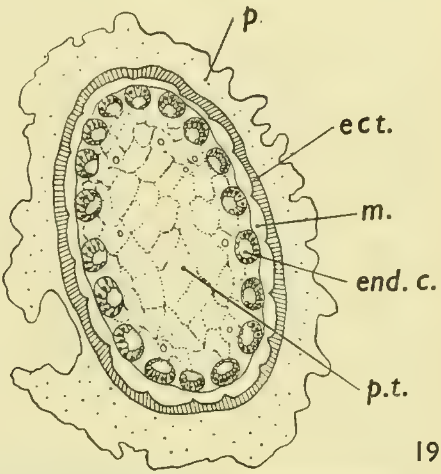

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FIG. 18. Diagrammatic longitudinal section of the hydranth of *Corymorpha nutans* (redrawn after Allman, 1872) ; it will be noted that the diaphragm is not reduced as in *Tubularia* (Fig. 17) and that the endoderm of the hydranth is continuous with that of the tentacle : *a.c.*, aboral chamber ; *b.*, blastostyle ; *ect.*, ectoderm ; *end.*, endoderm ; *endo.*, endocord ; *o.c.*, oral chamber ; *o.t.*, oral tentacle ; *p.*, parenchyma.

FIG. 19. Diagrammatic transverse section of the stem of *Corymorpha nutans* showing parenchyma and peripheral endodermal canals (redrawn after Stechow, 1909) : *ect.*, ectoderm; *end.c.*, endodermal canals; *m.*, mesogloea; *p.*, gelatinous perisarc; *p.t.*, parenchyma.

There is a slightly different arrangement in *Tubularia* where the posterior chamber has been eliminated and what remains of the stem canals open through a sieve plate

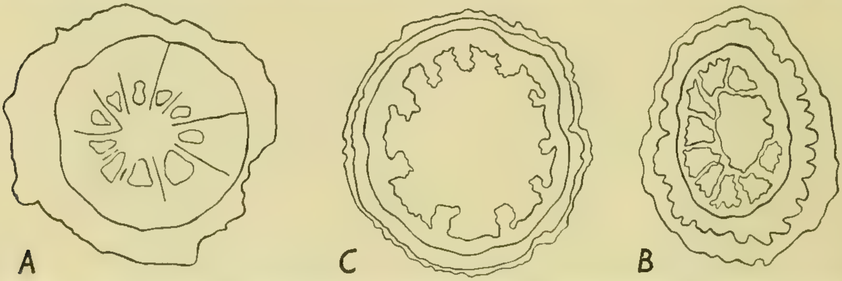


FIG. 20. Degeneration of the stem canals in *Tubularia* (simplified from Grönberg, 1898): A, sieve plate; B and C, transverse sections of stem.

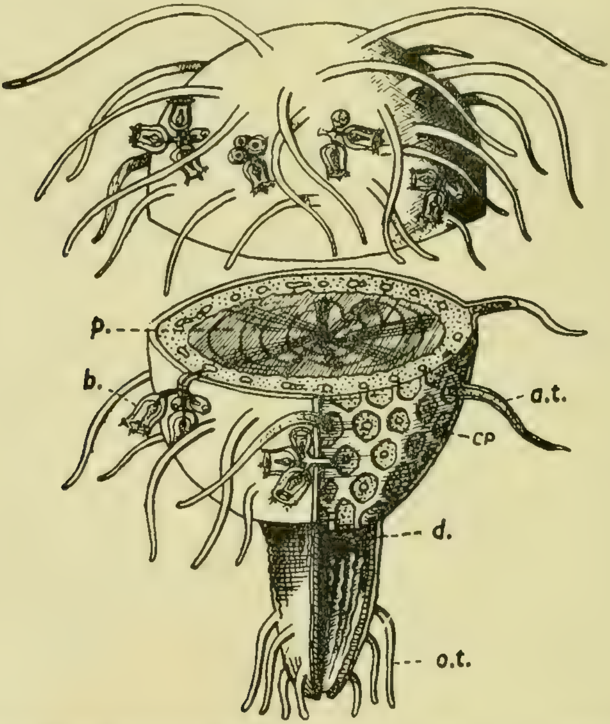


FIG. 21. *Pelagohydra mirabilis* Dendy (after Garstang, 1946); the lettering has been changed to conform to the interpretation given in this paper: *a.t.*, aboral tentacle; *b.*, blastostyles with developing medusae; *d.*, diaphragm; *o.t.*, oral tentacle; *p.*, parenchyma.

into the oral chamber (Text-fig. 20). The atrophy of the stem canals, inherited from a Corymorphine ancestor, in *Tubularia* may be associated with the development of a firm perisarc and with the much smaller diameter of the stem.

Garstang (1946, p. 126 and p. 184) follows Dendy in interpreting the swollen aboral end of the pelagic hydroid *Pelagohydra* as " the stalk region or hydrocaulus, with its axial parenchyma and peripheral labyrinth of canals", which, "has been dilated to form a kind of float and the hydranth with its oral tentacles is reduced ". This interpretation led Garstang into difficulties in his digressions into hydroid phylogeny. In all Tubularian and Margelopsid hydroids the gonophores are situated in the inter-tentacular region and I do not think that *Pelagohydra* is any exception (Text-fig. 21). Thus the float could be a dilated and much modified hind end of the hydranth in which the posterior whorl of tentacles and the ring of blastostyles have become scattered due to the swelling of this part of the hydranth into a float. Garstang homologized the canals in the float with the canals in the stem of *Corymorpha* but I do not think this is the right interpretation for as has been said, it implies that the float is cauline in origin. On the interpretation adopted here the float is the basal half of the hydranth in which the parenchyma supporting the diaphragm is enormously developed, eliminating not only the posterior (aboral) chamber but also almost completely obliterating the posterior half of the oral chamber leaving only canals for feeding the tentacles and the blastostyles.

Grönberg (1897, Taf 4, figs. 1 and 3) figures these canals in *Tubularia*, although

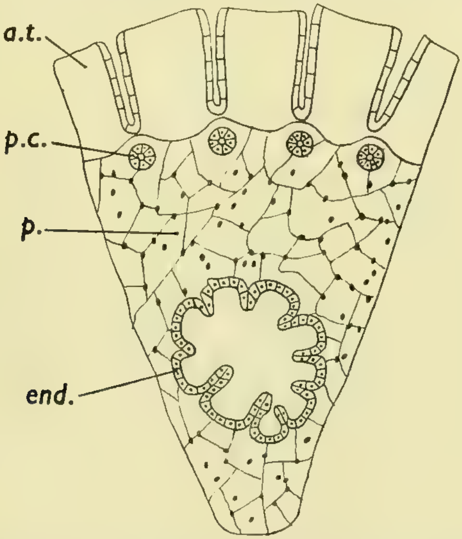


FIG. 22. Diagrammatic transverse section of a segment of the hydranth of *Tubularia* showing the peripheral canals which are continuous with the oral chamber of the hydranth (simplified from Grönberg, 1898) : *a.t.*, aboral tentacle ; *end.*, endoderm ; *p.*, parenchyma ; *p.c.*, peripheral canals.

Garstang does not seem to have noticed them (Text-fig. 22), and in his conclusions derives both the Tubulariidae and the Monocaulidae (i.e., *Branchiocerianthus*) from the Corymorphidae. In fact the structure of *Branchiocerianthus imperator*, described by Miyajima (1900) becomes intelligible when we relate it to that in *Corymorpha nutans*. At one stage in the evolution of *Branchiocerianthus* (Text-fig. 23), the diaphragm must have been so closely adpressed to the intertentacular wall of the hydranth by the development of the parenchymatous cushion as to become fused with it, leaving only canals for feeding the blastostyles and the tentacles (Text-fig. 24). Although Mark (1898) mistook this large hydroid for a Cerianthid, his remarks on these canals confirm the view that they are food canals: " Radial canals are traceable running across the disk from the base of the oral tube to the bases of the marginal tentacles, before reaching which many of them fork, each of the branches communicating with the lumen of a single tentacle ". In these species the aboral chamber has become large, possible due to the disappearance of most of the parenchymatous tissue (Text-figs. 23 and 24).

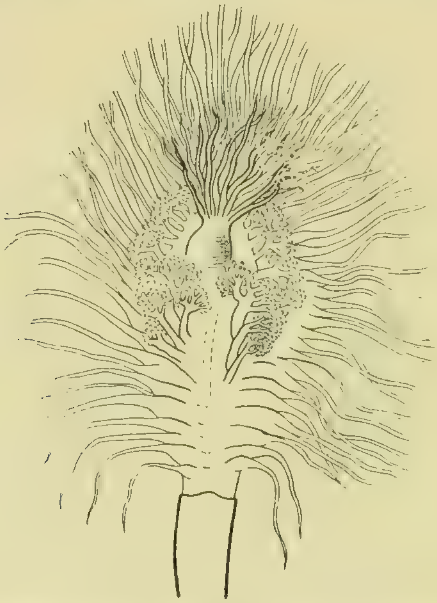


FIG. 23. *Branchiocerianthus urceolus* Mark: Oral face of bilaterally symmetrical polyp (simplified from Mark, 1898).

On the assumption that the float of *Pelagohydra* is cauline in origin, Garstang goes on to say (p. 184), " It is thus possible to imagine the sessile forebears of *Pelagohydra* as solitary Tubularias or Corymorphas, owing to the basal position of their gonophores and simple heads. There must have been—and may still be—a tribe of tall, simple, naked polyps rising from a creeping stolon with gonophores on their basal stalks, supported only by an endochordal axis ; and this tribe was presumably ancestral not only to *Pelagohydra*, but to all " Tubularians ". Here it appears that Garstang was deceived by the secondary simplification of many colonial hydroids into deriving solitary forms from colonial ones. The example which he quotes, *Gemmellaria* (*Zanclea*) and *Clavatella* (*Eleutheria*), are among the highest evolved forms in the Capitata. Similarly the erroneous suggestion that the gonophores were originally cauline (instead of being intertentacular in origin) is adequately treated on p. 471.

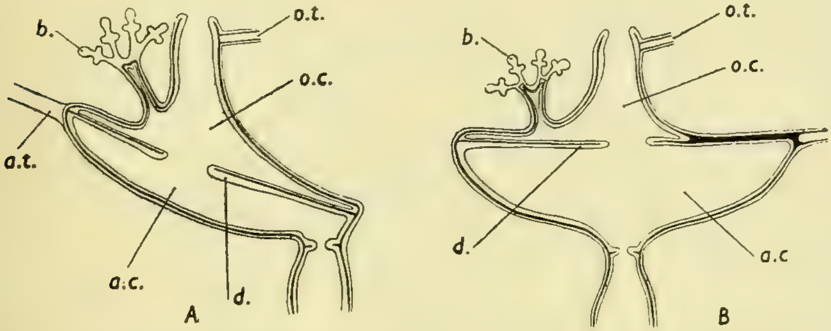


FIG. 24. *Branchiocerianthus imperator* (Allman) : hydranth redrawn from Miyajima (1900) : A, diagrammatic sagittal section ; B, diagrammatic transverse section : *a.c.*, aboral chamber ; *a.t.*, aboral tentacle ; *b.*, blastostyle ; *d.*, diaphragm ; *o.c.*, oral chamber ; *o.t.*, oral tentacle.

Garstang however came near to my own views at many points in his remarkable survey, for instance, " Without *Corymorpha* the structure of *Tubularia* would be unintelligible, and no one would suspect the secondary simplification which has led to *Pennaria* ". If he had realized the simplicity of the lower Corymorphines like *Euphysa* (*Corymorpha annulicornis*), and been less preoccupied with " cauline " gonophores in *Pelagohydra*, he would have recognized the significance of these forms in the phylogeny of *Corymorpha*, *Tubularia*, *Acaulis* and *Myriothela*.

Concerning *Myriothela* (*Arum*), Garstang (p. 145) seems to have erred in assuming that the branched coryniform blastostyles are vestiges of a once fully colonial life. These branched blastostyles are more likely to represent elaboration (often associated with large-sized polyps) in a solitary polyp, for the *Myriothela* line can be traced back through forms like *Acaulis* to a primitive Corymorphine (and all are solitary forms). The large egg and its unique clusters indicate a high degree of specialization in *Arum cocksi* (Text-fig. 15 p. 467).

It is not proposed to enlarge on the codonid relationships of the Disconanth Siphonophora here ; these have been discussed by Totton (1954) and Picard (1955).

(b) *Division of of labour in a colonial system*

Once the hydroid became a colonial form, the transport of food from polyp to polyp was assured by the continuous coenosarc. Among the many advantages it meant that the individual polyp need not be so large and could undergo secondary simplification. This is what I believe has happened in the deceptively simple polyps of the Corynidae where a large number of identical polyps carry on the function formerly undertaken by a solitary polyp.

The loss of the long aboral tentacles in the typical Corynids may be associated with the development of a bushy colonial habit where the long aboral tentacles could not be manoeuvred successfully. On the other hand they are retained in the Halocordylidae (Pennariidae) where the pinnate branching and the positioning of the hydranths allow these tentacles full play (Text-fig. 25).

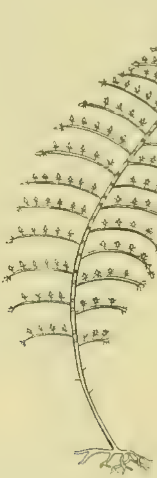


FIG. 25. The arrangement of hydranths on the upright, branched hydrocaulus of *Halocordyle* (*Pennaria*).

The colonial system, too, meant the beginning of specialization for particular tasks. In the Corynidae, which we may regard as among the simpler forms of colonial capitate hydroids, the polyps are all alike and perform the same functions, and it is only among the higher forms of corynoid polyps that we see this division of labour setting in. Some evidence for this differentiation was reported by Russell and Rees (1936) in the polyps of *Zanclea costata* Gegenbaur where it was noticed that there was some indication of division into nutritive and reproductive polyps, but it was also evident that towards the end of the budding period the nutritive polyps might also be transformed into reproductive ones.

Division of labour in the polyp has not progressed in the Capitata as a whole but in *Ptilocodium* and the Solanderiids some progress has been made. In *Ptilocodium* there are two kinds of polyps, the nutritive zooid (unarmed and without tentacles) which also bears the gonophores, and the dactylozooid or defensive zooid. The ordinary polyp no longer carries the gonophores and these are situated on the rhizocaulome formation in the Solanderiids like *Dendrocoryne.*

It is only when the more advanced Filifera are considered that we find the best examples of division of labour, where the different functions of feeding, budding of gonophores and protection, each have their own special kind of polyp. *Hydractinia echinata* (Fleming) is the classical example with nutritive, reproductive and two kinds of defensive zooid.

3. THE POSITION OF THE GONOPHORES

The position of the gonophores is, I believe, of limited significance in assessing whether a particular hydroid is primitive or advanced, but reflects general trends in the group. The position of the budding area between the two main whorls of tentacles on the body of the hydranth is one of the most constant (and essentially primitive) features of capitate hydroids. This position is the same in the primitive solitary hydroid and in the ancestral medusoid; as a budding area it involves no food transport problems because the food is either transferred direct through the wall of the stomach or passes into the lumen of the blastostyle which is in direct continuity with the stomach.

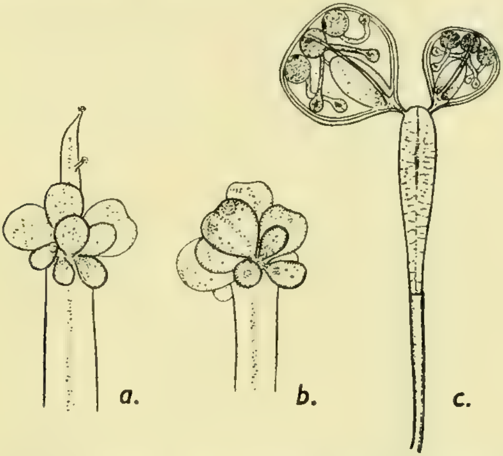


FIG. 26. Reduction of hydranths to blastostyles: A and B, *Zanclea costata* Gegenbaur; C, *Dipurena halterata* (Forbes) (after Russell & Rees, 1936; Rees, 1939).

There are however some serious disadvantages even though there are no food transport problems. When the hydranths are fertile and producing medusae or fixed gonophores in abundance (as they usually do in favourable circumstances) the hydranth itself becomes reduced to a simple blastostyle, without mouth or tentacles, due to reproductive exhaustion (Text-fig. 26). It means that most of the polyps of the colony must die down and become reorganized once more as

TABLE I.—*Position of Gonophores in the Filifera*

	On all hydranths	On selected hydranths	On special hydranths	On stem below hydranth	On stems	On stolons
Family Clavidae						
Clava squamata (O. F. Müller)	×	..	..	..	..	..
Merona cornucopiae (Norman)	..	..	×	..	..	..
Cordylophora lacustris (Pallas)	..	..	..	×	..	..
Turritopsis nutricula Brooks	..	..	..	..	×	..
Rhizogeton fusiformis L. Agassiz	..	..	..	..	..	×
Family Hydractiniidae						
Podocoryne carnea M. Sars	×	..	..	..	..	..
Hydractinia allmani Bonnevie	..	×	..	..	..	..
Hydractinia echinata (Fleming)	..	..	×	..	..	..
Family Cytaeidae						
Cytaeis japonica Uchida	..	..	..	..	..	×
Family Bougainvilliidae						
Dicoryne conferta (Alder)	..	.	×	..	..	..
Heterocordyle conybearei Allman	..	..	×	..	..	..
Bougainvillia linearis Alder	..	..	..	×	..	..
Bougainvillia muscoides (M. Sars)	..	..	..	..	×	..
Garveia nutans Wright	..	..	..	..	×	..
Aselomaris arenosa (Alder)	..	..	..	×	..	..
Rhizorhagium roseum (M. Sars)	..	..	..	..	..	×
Family Eudendriidae						
Eudendrium ramosum (L.)	×	..	..	..	..	..
Eudendrium capillare (Alder)	..	..	×	..	..	..
Family Pandeidae						
Leuckartiara octona (Fleming)	..	.	..	..	×	×

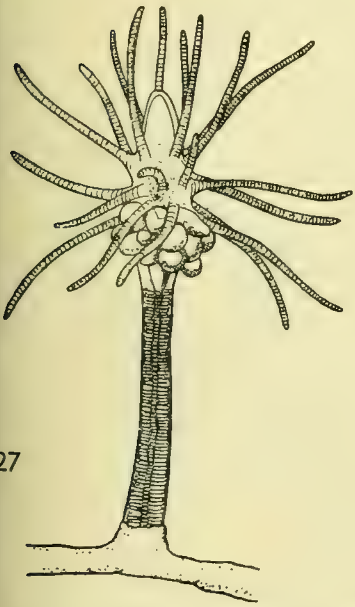
feeding polyps. Usually this involves an almost complete cessation of activity for many days. In high latitudes, for instance, this must curtail the already short breeding period in species near the temperature limit of their distribution.

Except in the aberrant Solanderiidae where the gonophores are not sited on the hydranth, most capitate hydroids conform to the above pattern. In *Eleutheria* (Text-fig. 48, page 500) and *Hydrocoryne* (Text-fig. 49, page 500), however, the gonophores have moved towards the base of the long polyps of these species, some distance from the chief digestive area.

In theory, at least, the adoption of a colonial habit, with stolonization and an erect hydrocaulus, would also mean the evolution of an efficient means of circulating food throughout the colony, so that it would no longer be necessary for the budding area to be in the immediate vicinity of the point of ingestion of food.

Except in some aberrant forms already mentioned, the Capitata have progressed little in this direction and it becomes necessary to choose examples from the Filifera.

The change in the position of the gonophores away from the hydranths is a general trend in the Filifera which is best illustrated in a table which gives examples of the different positions in which they are found (Table I).



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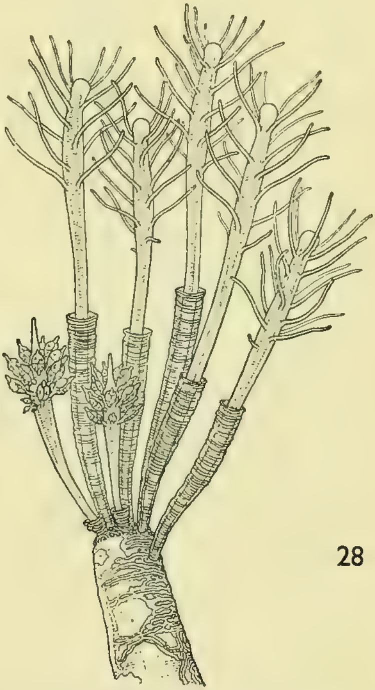

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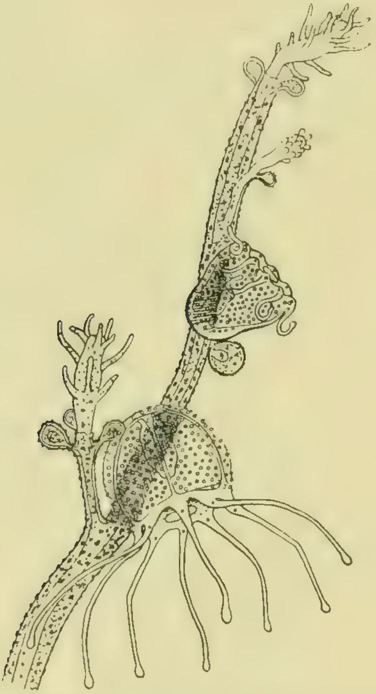
FIG. 27. *Clava squamata* Müller: gonophores are borne on all hydranths (after Vervoort, 1946*a*).

FIG. 28. *Merona cornucopiae* (Norman): nutritive and reproductive polyps are distinct from each other (after Rees, 1956).

In the Clavidae, one of the more primitive families of the Filifera, we find nearly all the steps in the transfer of the gonophores away from the hydranths. In *Clava squamata* all the hydranths bear gonophores (Text-fig. 27), but in *Merona cornucopiae*, division of labour has set in ; the nutritive polyps are able to concentrate on non-reproductive functions (Text-fig. 28). In *Cordylophora lacustris* the reproductive polyp has disappeared and the gonophore is borne directly on the hydrocaulus, a little way below the hydranth, and likewise, in *Turritopsis*, the medusa bud is borne directly on the hydrocaulus. (Text-fig. 29). Where there is little or no hydrocaulus the gonophore may be borne on the stolons as in *Rhizogeton fusiformis* (Text-fig. 30).



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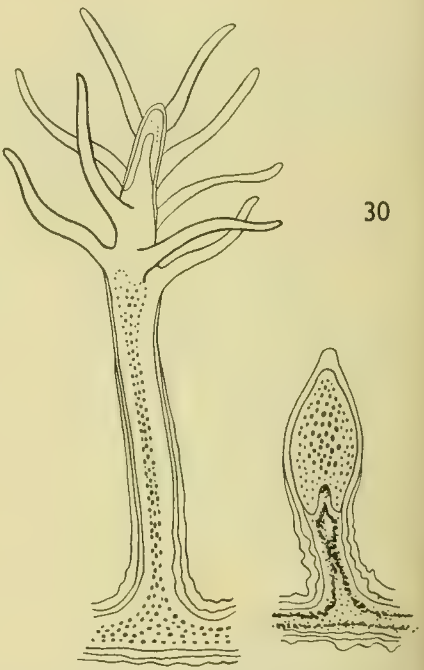

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FIG. 29. *Turritopsis nutricola* Brooks : a colonial Clavid hydroid in which the medusa buds are borne directly on the hydrocauli (redrawn from Brooks, 1883).

FIG. 30. *Rhizogeton fusiformis* Agassiz : hydranth and polypoid male gonophores (simplified from Agassiz, 1862).

In the family Hydractiniidae there is a similar range of positions, although species like " *Stylactella* " *elsae-oswaldae* Stechow which have gonophores arising from the stolons have not been included in the table. Any nutritive polyp may become a reproductive one in *Podocoryne carnea*, but in *Hydractinia allmani* Bonnevie it appears that only a certain number of polyps bear gonophores (Rees, 1956*b*), these differing only in size from the nutritive hydranths (if we make some allowance for reproductive exhaustion). *Hydractinia echinata* on the other hand has specially evolved reproductive polyps and the ordinary nutritive hydranths never bear gonophores.

The family Cytaeidae, which in some respects is intermediate between the Hydractiniidae and the Bougainvilliidae, has gonophores borne directly on the hydrorhiza ; in other respects, however, the family is not highly specialized (but see Rees, 1956*a*, p. 344).

In the higher groups of Filifera, only in a few members of the Eudendriidae like *E. ramosum* does the primitive condition, i.e., gonophores borne on the bodies of all the hydranths, persist, and even within this genus there is much diversity in their position.

In the other families, the Bougainvilliidae and the Pandeidae there are no surviving examples where gonophores are borne on the hydranths. Special reproductive hydranths comparable in function with those of *Hydractinia* are found in *Heterocordyle* and *Dicoryne* and these both have a specialized type of gonophore. In *Bougainvillia linearis* Alder (and also in *B. ramosa* and *B. superciliaris*), the budding area has moved away from the hydranth to the hydranth stalk which may carry several clusters of medusa buds. A more advanced condition is found in *Bougainvillia muscoides* where medusa buds are borne anywhere along the rhizocaulome formation (Rees, 1938).

Bougainvilliids with fixed gonophores exhibit a similar range of positions : *Aselomaris* (comparable with *B. linearis*), *Garveia* (with *Cordylophora*) and *Rhizorhagium* (with *Rhizogeton*).

These are only some of the examples which may be quoted but Table I demonstrates the evolutionary trend towards cauline gonophores, and it is also of considerable interest to note that individual species, within the same families and even the same genera, range from primitive to advanced positioning of gonophores. In this table the species which are considered to be the more primitive are placed at the top of the list and the more advanced towards the bottom of the list ; this assessment being based on consideration of both the hydroid and its gonosome. What emerges from this Table is that although the siting of the gonophores shows a broad evolutionary trend in the groups, individual species even within the same genus have progressed at different rates—some retaining the primitive condition while others have reached various stages in the direction of simple gonophores arising directly from the coenosarc and the elimination of the special reproductive polyp. This represents a small part of the mosaic.

4. EGGS AND ENCYSTMENT

(a) *Lecithotrophic and Planktotrophic Larvae*

In the naked hydroids egg sizes vary greatly and in general it can be said that those of the solitary forms are large while those of the colonial species exhibit a marked tendency to be small.

The large lecithotrophic eggs of *Corymorpha nutans* are typical; they are few in number, amoeboid and develop at the expense of nurse eggs on the manubrium. When the egg is finally cast out it may already have been fertilized and have secreted a thin pellicel around itself. Such eggs are 0·26–0·28 mm in diameter.

In *Hybocodon prolifer* the eggs are also large, amoeboid, and feed on nurse eggs but here they remain attached to the manubrium until they develop into quite large actinulae. *Tubularia* too for all practical purposes may be regarded as a solitary hydroid and here also in the sporosacs we find the development of a few actinulae at the expense of the other eggs. Actinulae are also found in at least one Corynid (*Actigia pusilla*) and in *Myriothela cocksi* there is an elaborate actinuloid larva; here the ripe egg is held by special "claspers" until the actinula reaches full development—this is the greatest degree of brood protection found in capitate hydroids.

The case is rather different in *Margelopsis haeckeli* where the larva develops into an actinula-like hydroid before being released from the manubrium of the medusa. In this species the eggs are thought to be parthenogenetic as no male gonads have ever been seen; this type of reproduction takes place in the summer. Later larger eggs are produced which develop as far as the stereoblastula stage on the manubrium and are then released, to settle on the bottom, becoming covered by a thin dome-shaped periderm; they are regarded as resting stages (Werner, 1954).

Eleutheria dichotoma, which may be regarded as an aberrant colonial Corynid, has a specialized cavity or brood pouch in the medusa where the small, non-amoeboid eggs develop into the planula stage. A similar sac has been reported in little known "Pteronemid" genera of medusae (*Pteronema*, *Ctenaria* and *Dendronema*).

In many of the Corynidae with well developed colonial habit, the eggs are usually small and develop into planulae after release from the sporosac or medusa. Brood protection in capitate hydroids thus reaches its highest development in the solitary forms but occasionally, as already noted, protection as far as the actinula stage is found in some colonial forms.

In the higher groups of Anthomedusae other than those with capitate hydroids we find surprisingly little by way of protection of brood. In the Clavidae, *Turritopsis*, for instance, retains the eggs on the manubrium of the medusa until they swim away as planulae and the same degree of protection is found in the fixed gonophores of some Bougainvilliid hydroids (e.g., *Aselomaris michaeli* Berrill, 1948).

The eggs of many Bougainvilliid medusae and related families are often quite small, numerous and develop after being shed into the water.

Typical egg sizes are noted in Table II opposite.

It has already been noted that as a rule the solitary hydroids have large yolky eggs, some measure of brood protection, and they frequently develop into an actinula, which, when it leaves the parent (hydroid or medusa) is ready to settle on the bottom. This can almost be termed non-pelagic development for the actinula's free existence in the plankton must be of very short duration.

By contrast, the smaller eggs (0·15 mm. or less in diameter) of most colonial athecate hydroids and medusae may be shed into the water as fertilized eggs or less

TABLE II.—*Egg Sizes in Anthomedusae and their Hydroids*

(Measurements in mm.)

HYDROIDS WITHOUT A MEDUSA PHASE

Solitary forms

Tubularia crocea Agassiz, 0·55 (Berrill, 1952).
Acaulis primarius Stimpson, 0·2–0·25 (Berrill, 1952).

Colonial forms

Hydractinia echinata Fleming, 0·15–0·2 (Berrill, 1953).
Aselomaris michaeli Berrill, 0·1–0·12 (Berrill, 1948).

MEDUSAE

Solitary forms

Corymorpha nutans M. Sars, 0·26–0·28 (Rees, 1937*a*).

Colonial forms

Stylactis hooperi Sigersfoos, 0·1–0·12 (Berrill, 1953).
Lizzia blondina Forbes, 0·08–0·12 (Rees, unpublished).
Rathkea octopunctata (M. Sars), 0·14 (Rees and Russell, 1937).
Bougainvillia britannica Forbes, 0·14–0·15 (Russell, 1953).
Bougainvillia superciliaris (Agassiz), 0·13 (Berrill, 1949).
Amphinema dinema (Péron and Lesueur), 0·14–0·15 (Rees and Russell, 1937).

frequently they may be retained on the manubrium or spadix until the planula stage is reached. On the assumption that the planula takes about two days to develop and may remain planktonic for a further two or three days, a free larval life of 4–5 days is envisaged.

Thorson (1950, p. 11) gave a fine account of the various types of larval development in invertebrates and discussed the ecological advantages and disadvantages of each type, but did not dwell on their evolutionary significance. The solitary capitate is seldom very small because it has to be of moderate size to carry out all its functions of nutrition and reproduction. The large yolky eggs of some Tubularians may only reflect the minimum size at which such a polyp can become self supporting and at the same time be a miniature of the adult.[1] With the progressive development of a colonial habit, the primary nutritive polyp can become functional at a much smaller size, permitting a smaller egg size, and an increased reproductive potential, together with greater possibilities for dispersal of young.

(b) *Encystment in Cnidaria*

As mentioned earlier (p. 480) it is only recently that it has become known that prolonged encystment of the fertilized egg takes place in any Capitate hydroid. As this phenomenon may have some bearing on the evolution of the attached, bottom dwelling hydroids, I propose to discuss it briefly from a wider viewpoint than covered by the title of this paper.

It has already been noted that the autumnal eggs of the pelagic tubularian

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[1] Dr. Bertil Swedmark has kindly pointed out that egg-sizes in the minute Cnidaria of the sand fauna bear no relation to the figures given here for the macroscopic forms.

Margelopsis haeckeli are larger than the summer eggs (Werner, 1955). Unlike the latter, they do not develop immediately into young hydranths, but form plano-convex cysts on the substratum and persist in this condition throughout the winter, giving rise in the spring to young pelagic hydranths (Text-fig. 31). This explains the sudden seasonal appearance of the hydroids and their medusae in the plankton of the southern North Sea for a short period in July and August. Here encystment for a considerable period of the year appears to be an essential part of the life cycle.

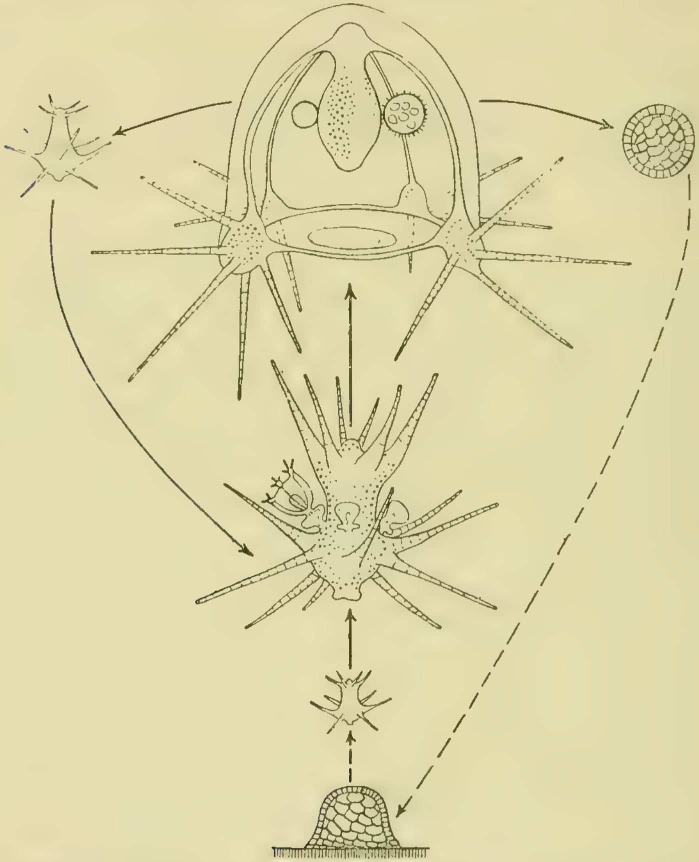

FIG. 31. The life cycle of *Margelopsis haeckeli* Hartlaub: summer eggs are small and develop into actinulae while the larger autumnal eggs pass through a winter resting stage (redrawn from Werner, 1955).

We do not know whether a cyst is formed by the primitive capitate hydroid *Tricyclusa singularis* (Schulze). In this species the hydroid suddenly appears in May-June and in some years becomes exceedingly abundant by asexual budding.

Then in July it develops fixed gonophores and by August has disappeared again until the following year. This seasonal appearance and the plano-convex form of the basal disk by which it is attached to the algal substratum suggests that it has an encysted winter stage, and that it may retain this disk as a means of attaching itself to the substratum without the aid of anchoring filaments (see Text-fig. 6 page 462).

Similar plano-convex cysts are formed by the hydroid of the limnomedusa *Ostroumovia inkermanika* according to Kramp and Paspaleff (1938, p. 35, figs. 10 and 11). It will have been noted (p. 480) that the newly fertilized eggs of *Corymorpha* are covered with a thin layer of perisarc, a condition normally associated with encystment, but here the young hydroid develops (at least in the laboratory) without any delay.

In the scyphomedusan genus *Cyanea* (as in many hydroids without lecithotrophic eggs) the fertilized egg develops into a planula first and encystment is rather variable. Hargitt and Hargitt (1910) in discussing the development of *Cyanea arctica* (regarded as a form of *C. capillata*) think that the encystment of the planula " is a condition often common where development is limited to the laboratory." They add: "whether such a condition ever occurs in nature we have no means of knowing, but so far as recalled it has not been made a matter of record. All observations point to the conclusion that the phenomena associated with encystment are expressions of adaptation due to unfavourable conditions of environment ". They note that McMurrich (1891) and Hyde (1894) differ about this.

McMurrich's account indicates that the majority of his planulae encysted, forming the typical plano-convex type of cyst, but that a few developed without becoming attached and without secreting a plano-convex cyst. My own observations (on *Cyanea lamarcki* Péron and Lesueur) agree with his in that " every young Scyphistoma was attached to a cyst, its stalk passing through the opening and spreading out on the lower flat wall." Hyde, on the other hand, noted encystment only in one embryo.

It is noteworthy that the Hargitts found that metamorphosis from planulae to scyphistomae after attachment took between 20 and 60 days, while some had not developed at the end of the period. They give figures of young scyphistomae suspended from their empty cysts, the latter acting as floats (Hargitt and Hargitt, 1910, figs. 38–41).

McMurrich stated that the encysted stage lasted for several days, while in my own experiments the young scyphistomae developed within 48 hours of settlement of the planulae.

Encystment in other Scyphozoa had been noted earlier by Kowalevsky (1884) in *Lucernaria*. The presence of a basal disk in *Stephanoscyphus*, the polyp-like scyphistoma of the Coronatae, also suggests that a cyst is formed here. The sum of these notes indicates that encystment is common to the Anthomedusae and the Limnomedusae in the Hydrozoa and to the Stauromedusae, the Coronatae and the Semaeostomeae in the Scyphozoa, although its occurrence has been noted in very few species.

It is of course well known that the egg may encyst in various species of *Hydra*, but encystment here may possibly have arisen in response to the need for such a device in fresh water where ponds are liable to dry up periodically.

We do not know enough about encystment in the Hydrozoa and Scyphozoa to assess its full significance but as already suggested the occurrence of the plano-convex cyst in widely divergent groups all exhibiting some kind of alternation of generations, may have a bearing on the evolution of the hydroid phase. Its elaboration from a resting stage, at first merely developing directly into a medusa, then gradually acquiring a polypoid form and budding daughter medusae, and evolving to a feeding polyp with tentacles can be readily envisaged, but is less attractive than the actinula theory for which there is more supporting evidence (but see p. 503).

5. THE DEVELOPMENT OF PERISARC

Before considering the development of the perisarc proper it may be appropriate to consider the phenomenon of the secretion of a thin pellicel by the fertilized egg in *Corymorpha*. This has been noted in *Corymorpha palma* (Torrey, 1907) and in *Corymorpha nutans* (Rees, 1937*a*) and seems to be the last surviving indication that encystment was a regular feature in the ancestral Corymorphines, but it has disappeared completely in species like *Tubularia* in which the egg develops directly into an actinula on the manubrium of the sporosac.

The way in which the eggs of *Corymorpha* attach themselves to the substratum is also significant. In *Corymorpha nutans*, " The pellicel of the egg is very elastic and is pushed out into broad pseudopodia-like growths on the underside into contact with the substratum to which the pellicel adheres. The so-called ' pseudopodia ' then withdraw into the main body and the dilated pellicel shrivels up into a small tube. Several of these may be formed (Text-fig. 32) and they anchor the egg to the substratum. They may be termed anchoring filaments. The young developed

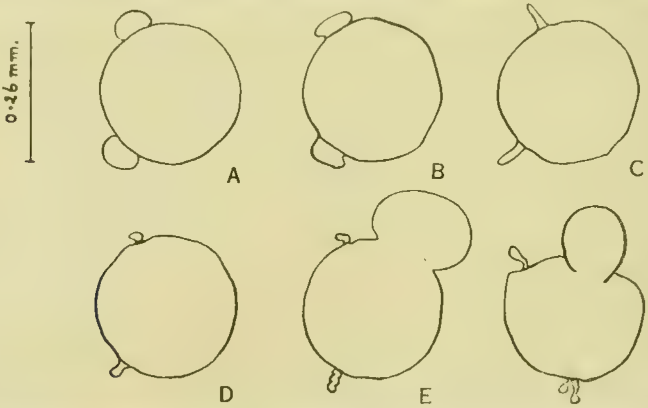

FIG. 32. *Corymorpha nutans* M. Sars : successive movements during the attachment of the pellicel of the egg to the substratum by anchoring processes (after Rees, 1937*a*).

directly out of the eggs into young polyps" (Rees, 1937*a*, pp. 743–744). In *C. palma*, however, Torrey notes that after hatching out the larva wanders about before settling. In both species it will be noted that the period of encystment is very brief and that the pellicel is very thin. What is of great interest however is the mode of anchoring the egg which is analogous to the development of filaments for anchoring in the mud living polyps of *Corymorpha*, *Euphysa*, *Hypolytus*, *Acaulis* and some species of *Myriothela*.

In the evolution of the hydroid phase culminating in the complex Sertulariidae and Plumulariidae, with the total suppression of the medusa phase, we see a gradual increase in the complexity of the perisarc ; this becoming very important as an elaborate framework for the arrangement of the hydranths.

In the solitary hydroids the perisarc is either feebly developed or remains fairly simple. I am inclined to believe that the most primitive hydroids had little or no perisarc and in the simpler forms we have a condition approaching this in the lower Corymorphines and in *Tricyclusa*.

Mud-living forms like *Euphysa*, *Hypolytus*, *Amalthaea*, and *Acaulis* have a feebly developed, poorly chitinized perisarc which forms a loose sheath around the stem of the polyp. It is a rather gelatinous structure, to which mud particles adhere, and can be discarded if necessary, and a new one secreted by the polyp. *Corymorpha nutans*, which lives on firmer sandy or sandy-mud substrata, has a more closely-adherent perisarcal sheath. Associated with this rudimentary tube are a number of filaments which are used for anchoring the polyp ; they are also covered with perisarc and their tips become attached to grains of sand or other firm particles, so anchoring the organism. Typically they form a basal tuft at the base of the stem.

In the lower Corymorphines, such as *Hypolytus* and *Euphysa*, the filaments are quite few. Here the stem is known to become constricted off into a number of asexual bodies, sometimes leaving only the hydranth when the process is completed (Text-fig. 33). In these polyps the rudiments of filaments are always found in a ring around the posterior border of the hydranth below the aboral tentacles (Text-fig. 34). This may be the ancestral position of the filaments and it appears that these lie near a zone of growth, and so with the development of a new stem, are carried away from the hydranth proper.

To return for a moment to the actinula, it is possible to imagine an ancestral form, drifting over the sea bottom, anchoring itself by aboral processes, these evolving into the well known anchoring filaments (analogous to those of the eggs of *Corymorpha*). The position of these processes on the hydranth in the primitive Corymorphines suggests that they may have arisen by modification of some of the tentacles of the actinula. However, whatever their origin, the anchoring filaments and the loose, semi-gelatinous sheath, are primitive features found only in solitary hydroids.

The full development of anchoring filaments is best seen in the higher Corymorphines, where, in *C. nutans* and related forms, there is an enormous tuft at the base of the stem ; this firmly anchors the polyp in sand or sandy mud and represents the highest development of this mode of anchoring. Occasionally too, the filaments

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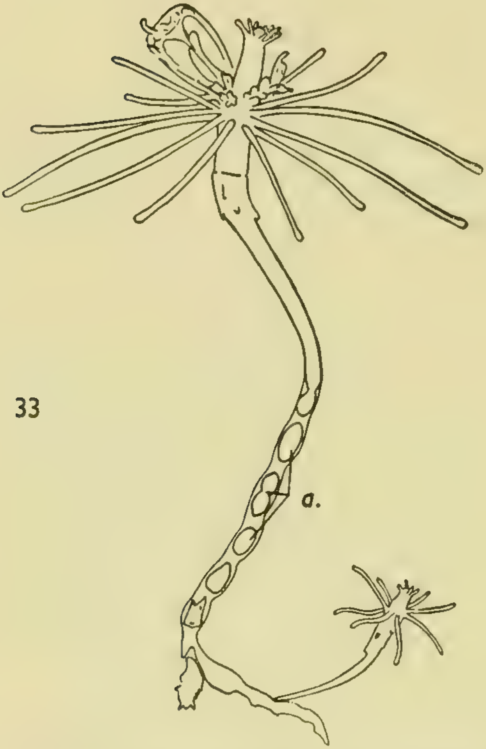

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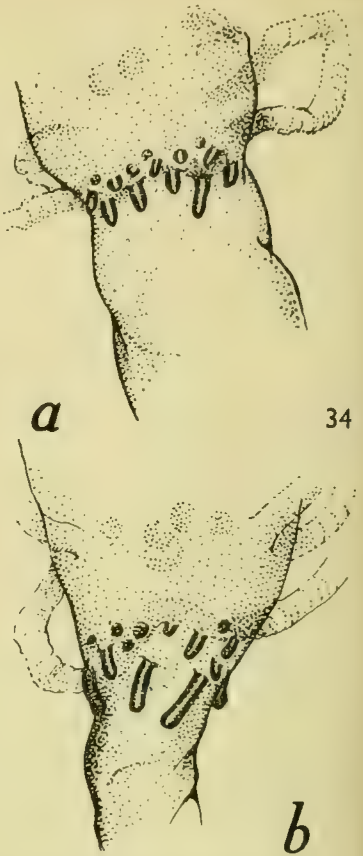
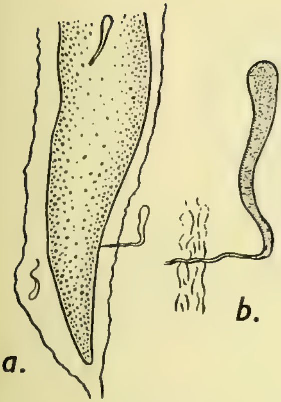


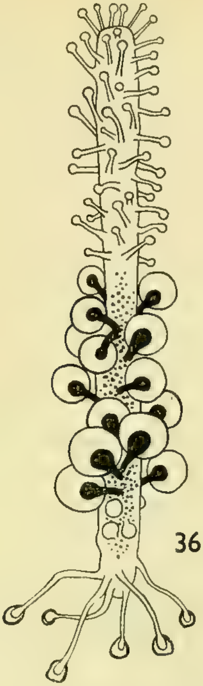
Fig. 33. *Euphysa farcta* (Miles): a simple Corymorphine in which the stem becomes constricted off into a number of asexual bodies (redrawn after Miles, 1937): *a.*, asexual bodies.

Fig. 34. *Euphysa aurata* Forbes: posterior border of hydranth with rudiments of filaments, A, Trondheimfjord (Fillan-fil-fjord, between Hitteren and Fjeldväröy), dredged 150 m., 21.viii.1937; B., Trondheimfjord (Strindfjord), dredged 90 m., 21.viii.1937: both collected by Dr. Jöran Hult.

can give rise to young polyps (Text-fig. 35) which become cut off during their growth from the parent. This may perhaps be a reminder of the way in which some simpler ancestor developed stolons and so gave rise to the colonial Corynidae and their allies.

In *Acaulis primarius* the gelatinous tube and the filaments are retained but in several species of *Myriothela* including the northern *Myriothela phrygia* (Fabricius), the tube is lost and only the filaments are left for anchoring (Text-fig. 36). These are chitinized and their mode of attachment has been described by Manton (1940





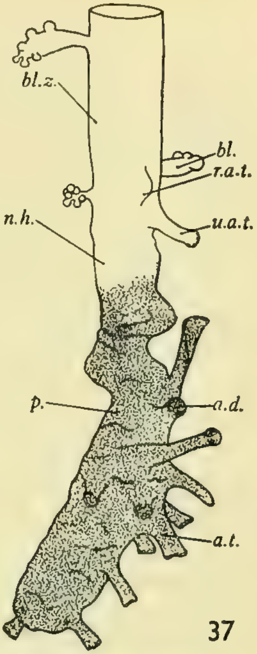


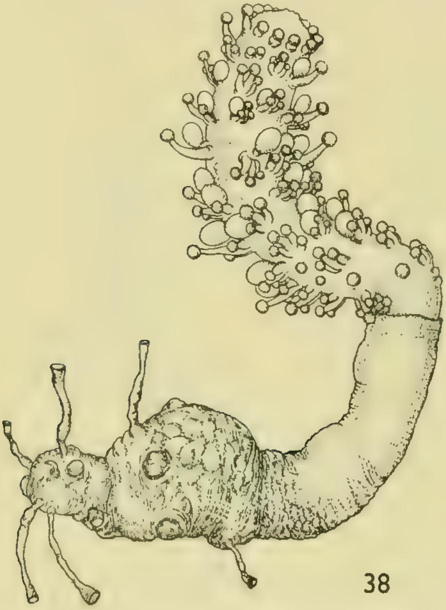
FIG. 35. Young polyp beginning to differentiate from a frustule in *Corymorpha nutans*; from a specimen in Zoologiske Museum Copenhagen (taken at Frederikshavn, 27th July, 1931).

FIG. 36. *Myriothela phrygia* (Fabricius): note the naked polyp with perisarc only on the dilated ends of the anchoring filaments (redrawn from Sars, 1877); for the sake of clarity only half the capitate tentacles have been shown.

FIG. 37. *Arum cocksi* Vigurs: lamellar basal perisarc with modified anchoring filaments (after Manton, 1941).

and 1941) in detail. Had Manton been familiar with those of *Corymorpha* she would have recognised that her description of the "adhesive tentacles" of *Myriothela phrygia* in the following terms: "many of them appear to have shrunk in diameter, so leaving the terminal disk of the attachment appearing much wider than the stem" applied also to the filaments of *Corymorpha*. There is no doubt that they are homologous.

Arum cocksi presents an interesting transitional stage as regards perisarc between the filament type of anchoring and the development of a firm adherent perisarc. In this species the basal portion of the hydranth is covered by perisarc, which according to Manton (1941) is roughly cylindrical in shape, but distorted to fit irregularities of the substratum (Text-fig. 37). Here the anchoring filaments are short, finger-like projections from the surface of the perisarcal sheath (the hydrorhiza of Manton) with flattened disk-shaped ends which adhere to the substratum in the manner described by Manton, that is, " the chitin forming a disk of adhesion is thick, and is attached to the mesogloea of the tentacle ". Some evidence is put forward by Manton which suggests that in *Obelia*, for instance, the mode of attachment of the stolons is different and that no mesogloea is involved, but for the simpler capitate forms we have no evidence of what happens.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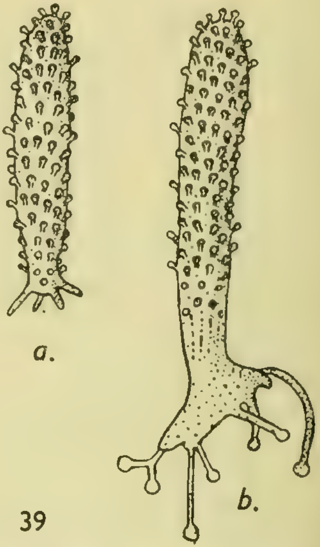
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FIG. 38. *Monocoryne gigantea* (Bonnevie) : sketch of a syntype from Hammerfest in the Zoologisk Museum, Oslo. Note the tubular basal perisarc and the few stout anchoring filaments.

FIG. 39 A and B. *Arum cocksi* Vigurs : regeneration and attachment to substratum by means of anchoring filaments (after Billard, 1921).

Here may also be mentioned *Monocoryne gigantea* (Bonnevie), a rather aberrant species, which, while having some obvious affinities with *Myriothela*, stands rather on its own in the *Acaulis-Myriothela* group of hydroids. As regards development of perisarc it shows an interesting transitional stage, the lower part of the polyp being clothed in a sheath of perisarc, which is much firmer and more closely adherent to the polyp itself than in *Acaulis* and has a few strong filaments at the base for attachment (Text-fig. 38). These features were noted during a re-examination of Bonnevie's two specimens in the Zoologiske Museum, Oslo in 1955. I was not able to ascertain whether any of the basal perisarc of the polyp itself could be termed adherent.

Regeneration and the re-attachment of the cut stem of *Arum cocksi* by means of filaments (Text-fig. 39) without the preliminary formation of a basal sheath has been described by Billard (1921). In this species the proximal end of the mutilated polyp puts out several processes which attached themselves to the substratum just as the filaments of *Corymorpha* do. In the higher Filifera, in *Amphinema dinema*, for example, the settling planula almost invariably puts out a three-rayed stolon to fix itself on the bottom and I am inclined to regard these rays as homologous with anchoring filaments—the latter being primitive and to be regarded as forerunners of true stolons.

Tricyclusa singularis, as an unique survivor of an aberrant group of early capitate hydroids, has a very interesting kind of perisarc. The hydroid is solitary and is attached to the surface of seaweeds and *Zostera* by a pedal disk, comparable to what is found in the hydroid of the Limnomedusa *Ostroumovia* and in young scyphomedusan scyphistomae. Distally this expands into a dilated, poorly-chitinized sheath into which the hydranth is partially retractile. The gelatinous sheaths in *Euphysa*, *Corymorpha* and *Tricyclusa* are clearly homologous because all three genera are obviously derived from the same early Corymorphine ancestors (but see p. 514).

It is only in these aberrant survivals that we see nature's experiments in the direction of a firm perisarc, but this essential step preceding the development of a colonial habit must have taken place in a comparatively unspecialized Corymorphine ancestor, in which the capitate oral tentacles were retained and in which the aboral whorl had already become filiform. The larva of *Corymorpha nutans* is rather like this and except in its stem and mode of anchoring is rather similar to young polyps of colonial corynid hydroids like *Stauridiosarsia* and *Cladonema*.

This evolution of firm perisarc probably accompanied the change from a soft mud or sandy habitat to a firm substratum and meant the disappearance of the typical filament, or it might be said that the filament became transformed into a permanent structure, the creeping stolon, attached along its entire length to the substratum. This enabled a firm perisarc to be evolved, and this in turn, provided the secure holdfast required for elaboration into a colony with polyps at intervals along the stolon. The evolution of firm perisarc, too, meant that it could acquire definite shape, such as ringing and internodes. These in turn depend on the way growth takes place as indicated by Berrill (1952) in the following terms: "Growth occurs rhythmically, or in pulses, which when in slow succession becomes recorded by the polymerizing perisarcal chitin as annuli. When occurring in rapid succession, the perisarcal annuli have no time to form, and straight perisarc results. The alternation of annular and internodal perisarc is indicative of a major rhythm of growth superimposed on the basic pulsation."

6. THE MEDUSA OF CAPITATE HYDROIDS

In this group (the Codonidae of Haeckel) it is generally agreed that the medusa is among the simplest in the hydromedusae, although it must be admitted that there are also some highly specialized and rather aberrant forms especially in the Cladonemidae and Eleutheriidae.

The ancestral Codonid can be envisaged as having a deep bell-shaped umbrella with nematocysts, either scattered over the exumbrella, or arranged in perradial tracks (Text-fig. 40). The stomach would be tubular with a simple circular mouth and the gonad would completely encircle the stomach. Four radial canals, a ring canal and four perradial tentacles complete the picture of the ancestral codonid and few would disagree with this interpretation. To this, I would add that the tentacles were probably moniliform and it is possible that budding of daughter medusae from the stomach would take place before maturation of the gonads. Medusae of the genus *Sarsia* are recognized as departing but little from the generally accepted idea of a simple codonid but two features require comment.

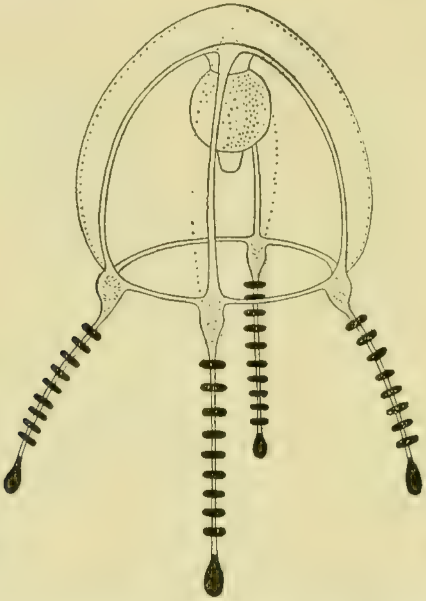

FIG. 40. Diagrammatic representation of an ancestral Codonid medusa with ring gonad, exumbrellar nematocyst tracks and four perradial tentacles with moniliform arrangement of nematocyst batteries.

The more usual arrangement of nematocysts on the exumbrella is the scattered one, but there are some nematocyst tracks in various forms, *Ectopleura* (Text-fig. 41) and *Hybocodon* (Text-fig. 42) in the Tubulariidae, *Neoturris* in the Pandeidae, and special tracks in *Zanclea* and various "pteronemids" and *Proboscidactyla stellata* (Limnomedusae);[1] all are widely divergent forms and and this may imply the persistence of an ancestral character (see p. 504).

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[1] The type of nematocyst track found in *Zanclea* is also found in the *Chrysomitra* medusae of the Chondrophora which are believed to have a Capitate ancestry (Totton, 1954; Picard, 1955).

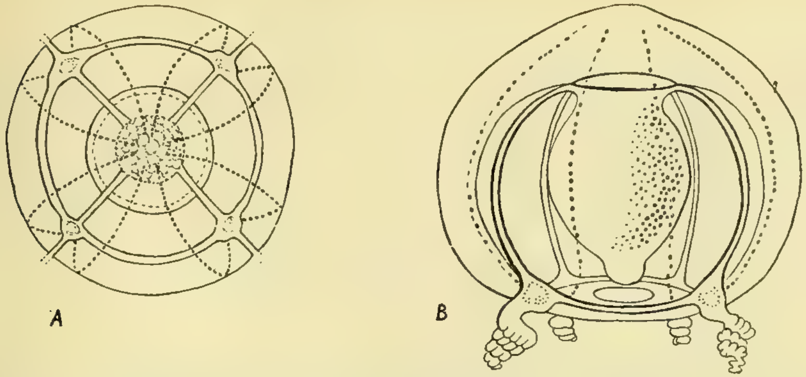
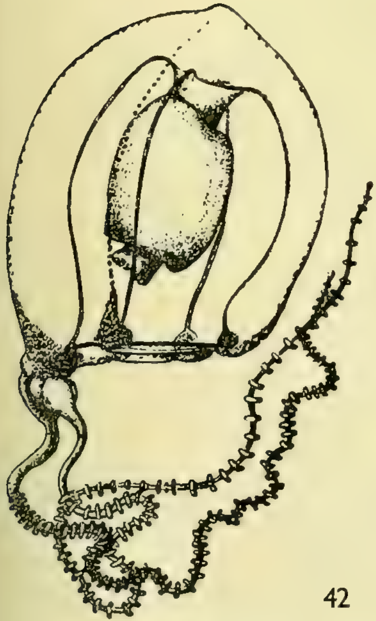


FIG. 41. *Ectopleura dumortieri* (van Beneden): A, apical view of medusa with 8 nematocyst tracks; B, side view of medusa (redrawn after Russell, 1953).



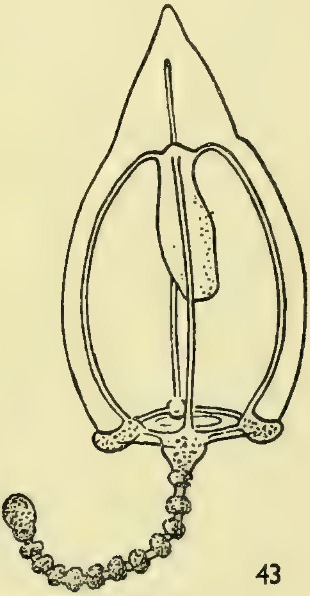


FIG. 42. *Hybocodon prolifer* L. Agassiz: medusa (after Hartlaub, 1907). Note the exumbrellar tracks and the moniliform arrangement of nematocysts on the tentacles.

FIG. 43. *Corymorpha nutans* M. Sars: young medusa with partially extended tentacle (after Russell, 1953).

There is much evidence for regarding the moniliform arrangement of the nematocyst batteries on the medusa tentacle as a primitive character. This arrangement is retained in its most perfect form in *Corymorpha*, (Text-fig. 43) *Euphysa* (Text-fig. 44) and *Hybocodon*, but as already noted it is only in *Euphysa*[1] that this condition exists in both hydroid and medusa (Text-fig. 5, page 460). This type of tentacle is found in other families of the Capitata in a reduced or modified form, but in the Filifera with further reduction and scattering of the nematocysts, traces of the original moniliform arrangement are lost.

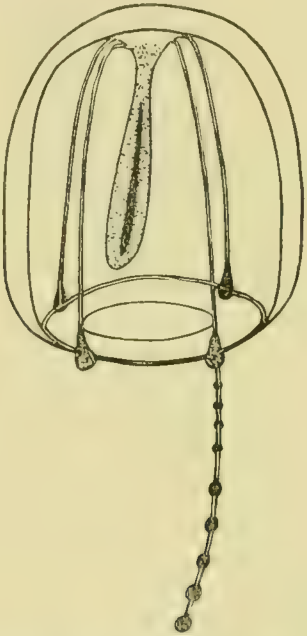


FIG. 44. *Euphysa aurata* Forbes: newly liberated medusa with extended moniliform tentacle (after Hult, 1941).

Even in the Tubulariidae this arrangement becomes modified in *Ectopleura dumortieri*, and in *Gotoea typica* the armature becomes reduced to a single terminal knob. It is in the Corynidae that the reduction is best seen in *Sarsia eximia*, *Dipurena halterata*, *Dipurena ophiogaster* and in *Sarsia prolifera*. In *Dipurena strangulata* (McCrady) there is only a single terminal knob. (Text-fig. 45).

There is doubt whether the grouping of nematocysts into half rings or spiral clasps in many Limnomedusae arose from the moniliform arrangement; there is however a tendency for them to be moniliform in the hydroid *Annulella gemmata* (Ritchie, 1915) and in the medusa *Gonionemus vertens* (Russell, 1953, p. 400, fig. 263).

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[1] *Mocrisia* and other related forms are excluded from discussion in this paper for their status requires elucidation.

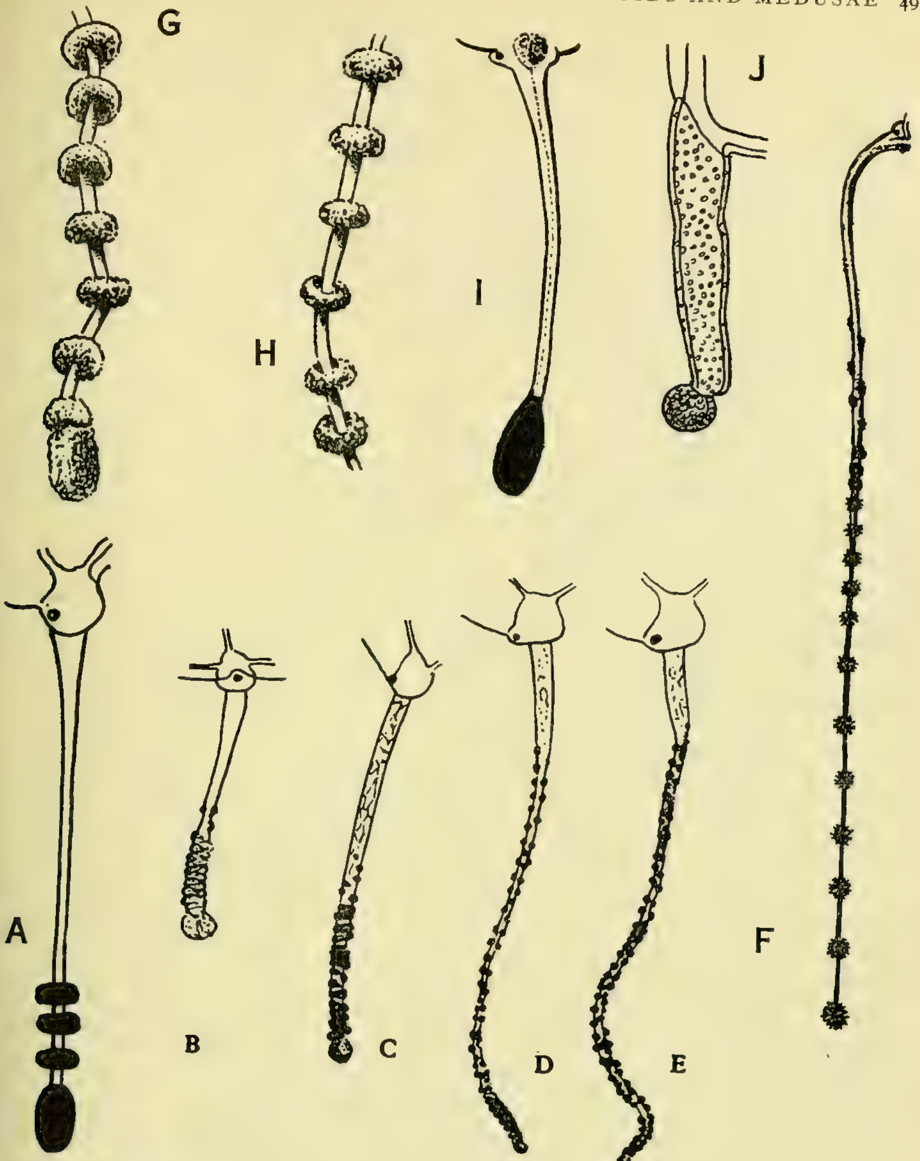

FIG. 45. Stages in the reduction of the moniliform tentacle in capitate medusae: A, *Dipurena halterata* (Forbes); B and C, *Sarsia gemmifera* Forbes; D, *Sarsia prolifera* Forbes; E, *Dipurena ophiogaster* Haeckel; F, *Sarsia tubulosa* (M. Sars), juvenile; G, *Corymorpha nutans* M. Sars; H, *Euphysa aurata* Forbes; I, *Dipurena strangulata* McCrady; J, *Gotoea typica* Uchida: A and I, (original); B–E, G and H, (after Russell, 1953); F, (after Allman, 1872); J, (after Uchida 1927).

It has always been recognized that the aboral tentacles of the tubularian actinula can be homologized with the marginal tentacles of the medusa. It follows that the stomach of an Anthomedusan (where budding takes place and the gonads develop) corresponds to the region immediately anterior to aboral tentacles in the hydroid—and this is the region where these activities take place in the Capitata in general.

Budding of daughter medusae from the manubrium is the more common method seen in Anthomedusae (e.g., *Eucodonium brownei* and *Sarsia gemmifera* in the Capitata, and *Lizzia blondina* and *Rathkea octopunctata* in the Filifera). Less commonly there may be budding from tentacle bulbs on the bell margin (as in *Hybocodon prolifer* and *Sarsia prolifera*). This seems to be a less primitive site for budding than the manubrium. In the latter ingested food is absorbed and made immediately available on the spot for building up the tissues in budding ; there are no transport problems as in *Sarsia prolifera* where food has to be carried along the radial canals to the tentacle bulbs for use there. In this respect perhaps *S. prolifera* may have evolved a more efficient means of dispersing food along its radial canals thus enabling it to produce medusa buds at some distance from the point of ingestion and its swimming movements are unhampered by having the subumbrella cavity filled with young buds.

The evolutionary significance of the development of an efficient means of dispersing food in the hydroid is discussed on p. 477.

The mouth is simple without armed lips or oral tentacles in most Codonid medusae and this is generally regarded as the primitive condition. In the hydroid of the Tubularians (Tubulariidae and Corymorphidae) the oral whorl appears late in the development of the actinula and must be regarded as a secondary character evolved in the primitive Corymorphine hydroids.

In the higher Anthomedusae the mouth of the medusa may become armed in various ways. This may take the form of lips armed with nematocyst clusters as in *Cladonema* (Plate 13, figs. 7 and 8) and the Hydractiniidae, or the lips may become frilled and armed with a continuous band of nematocysts along their free margin as in *Turritopsis* or there may even be simple or branched tentacles situated close to the mouth as in *Bougainvillia.*

Branching in the medusa tentacle is found in the Cladonemidae and the Eleutheriidae ; in the latter the tentacle bifurcates, the one branch carrying an adhesive organ and the other a nematocyst cluster at its tip. In *Cladonema* however, the tentacle is branched and part of it may be said to be coryniform just as in the tentacles of the hydroid *Cladocoryne* (Text-fig. 54, page 511) and the blastostyles of the hydroid *Arum cocksi.* The appearance of this type of tentacle in *Cladocoryne* and *Arum* is a feature which provides a link between these two forms but it is not sufficient evidence to prove that *Cladocoryne* has an Acauloid ancestry. This tentacle, in the *Cladonema* medusae, seems to have arisen independently for the *Cladonema* hydroid cannot be derived from a myriothelid stock.

Mention must also be made of two other features of specialized medusae. There is a tendency in the Filifera for the gonads on the manubrium to become split up. In the Capitata this condition is found in *Gotoea typica* (tentatively placed in the

Tubulariidae by Uchida) and in *Zanclea* where the gonads are split into four interradial groups. In *Eleutheria*, to quote Mayer (1910, p. 93), " There is a peculiar brood pouch above the stomach but this pouch is not connected with the gastrovascular cavity of the medusa. The cavity of this brood pouch is, however, connected with the bell cavity by means of simple, interradial openings. The products are developed exclusively in the epithelial lining of this brood pouch, which is derived from the ectoderm of the subumbrellar cavity of the bell ". (Text-fig. 48, page 500).

Eleutheria is of course highly modified for an ambulatory existence on seaweeds but similar brood pouches have been described in *Pteronema*, *Ctenaria* and *Dendronema*.

7. THE VALUE OF THE GONOPHORE IN CLASSIFICATION

Widely divergent opinions have been held about the value of the gonophores in the classification of this group, and much of the confusion in classification at generic level is due to the lack of unanimity on this score. Early authors notably Allman (1864) laid particular stress on whether the gonophore became free, as a medusa, or remained fixed, as in a sporosac, and this is broadly also the view of Stechow (1919, 1923). Allman even goes further in saying " each of these forms of gonophore may itself present differences which will afford characters of value in the limitation of our genera ". This implies, and was often subsequently interpreted as meaning, that differences in the degree of reduction of the gonophore (eumedusoid, cryptomedusoid, heteromedusoid and styloid kinds) could be used to distinguish genera (Text-fig. 46). These types of gonophore were regarded as important in the definition of genera by Kühn, but he was not always consistent, for he used them as specific characters in the genera *Podocoryne* and *Hydractinia* (1913, p. 227).

At the other extreme, Levinsen (1893) believed that no generic distinction should be drawn between hydroids that were co-generic on hydroid characteristics, even if some gave rise to free medusae and others to fixed gonophores. Indeed there is much to commend this approach to the specialist who only knows his species as something dead in a bottle.

It is to Broch (1915, 1916) that we owe the most lucid account of the bearing of the gonophores on classification. He demonstrated very clearly that the degree of reduction of the gonophore was most unsuitable as a generic character because of sexual dimorphism, for he was able to show that the male gonophores might be more reduced than the female ones, as in some species of *Tubularia* (Table III).

Broch was also concerned with the status of genera like *Coryne* and *Syncoryne*, *Hydractinia* and *Podocoryne*, where the sole criterion is assigning species to one or the other is whether they have fixed or free gonophores. Following Levinsen he merges the genera, as does Kramp (1935*a*) for *Corydendrium*. Kramp (1949) supports Levinsen's views in the following terms : " I wish to state that the degree of development or reduction of the gonophores is not a generic character " and adds that a line should not be drawn between two groups of species merely on account of

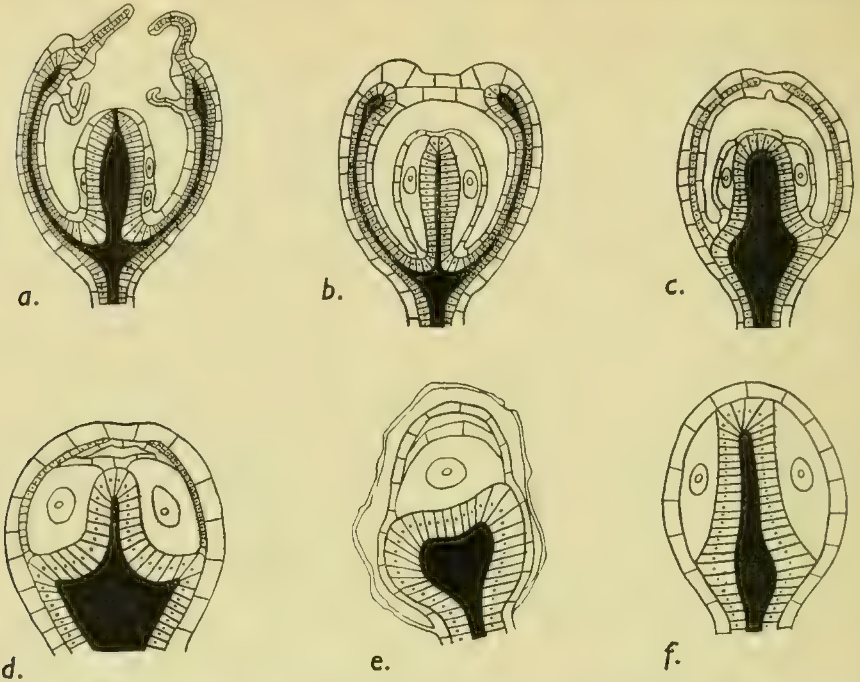

FIG. 46. Diagrammatic longitudinal section of the different stages in the reduction of the gonophore: A, medusa; B, eumedusoid; C and D, cryptomedusoid; E, heteromedusoid; F, styloid (redrawn from Kühn, 1913).

TABLE III.—*Degree of Reduction of the Gonophores*

	Medusa.	Eumedusoid.	Crypto-medusoid.	Styloid.
Corymorpha nutans M. Sars	×	..	..	..
Corymorpha glacialis G. O. Sars	..	♂ + ♀	..	..
Corymorpha groenlandica Allman	..	..	♂ + ♀	..
Tubularia indivisa L.	..	♀	♂	..
Tubularia larynx Ellis & Solander	..	♂ + ♀	..	..
Tubularia regalis Boeck	..	♀	♂	..
Ectopleura dumortieri (van Beneden)	×	..	..	..
Hybocodon prolifer L. Agassiz	×	..	..	..

the gonophores being developed into free-swimming medusae or remaining in connection with the hydroid polyp (the trophosome) as fixed gonophores if no other structural differences imply a generic separation". This scheme works very well and is indeed admirable if each group of species fell naturally into one type of hydroid and one type of free medusa. There are, however, serious difficulties which make it unworkable in many families. Let us first consider the simple examples shown in Table III of *Tubularia*, *Ectopleura* and *Hybocodon*, where the second and third genera have free medusae each entitled on its own characteristics to generic rank. The *Hybocodon* hydroid is a little less like *Tubularia* than that of *Ectopleura* so that presumably *Ectopleura* could be merged with *Tubularia* although there is no absolute certainty that Tubularian gonophores have been derived by reduction from *Ectopleura* medusae.

As Kramp states: " The medusae *Sarsia*, *Dipurena*, *Linvillea* and *Zanclea* all have polyps resembling *Coryne*, and among the Pandeidae the medusoid genera *Amphinema*, *Halitholus* and *Leuckartiara* all have very similar hydroids. Moreover, the hydroids of these Pandeidae are very similar to those of *Bougainvillia*, though the medusae belong to two different families ". In all these groups the problem is the same for we must recognize that the generic differences established for the medusae are sound ones, and in this connexion I cannot agree with Broch (1916) who is disinclined to pay much attention to the free medusae in the classification of hydroids, " On account of their dependence on the outward conditions and their power of plastic accommodation to biological influences, the gonophores are unsuitable for basis of division into genera ". But the medusa, evolved as it is for life in a planktonic environment, is an essential part of the organism and leads to a better appreciation of the mosaic representing the whole species.

To return to the problem of the species with fixed gonophores, do we link *Coryne* either with *Sarsia*, *Dipurena* or with *Linvillea* or even found a broad Levinsenian genus which embraces all four genera? Similarly do we unite *Rhizorhagium* with *Bougainvillia* in the *Bougainvilliidae* or with one of the genera *Amphinema*, *Halitholus* or *Leuckartiara* in the Pandeidae. The study of their nematocysts may enable us to ascertain the family status of problem species but so far it shows no great promise for distinguishing genera. Levinsen's theoretical approach cannot be implemented now and there are other considerations which would make any naturalist hesitate to unite genera like *Coryne* and *Sarsia*,[1] even though we have forms like *Coryne lovéni* in which the medusa is fully formed but never released. Each transitional species like this has to be classified on its medusa structure and this species appears to be sufficiently close to *Sarsia* in its morphology to be placed in that genus, and that is where I would classify it. But who knows whether *Coryne pusilla* Gaertner with styloid gonophores is co-generic with it?

Let us consider the free medusa, not as an organ only a little removed from the fixed eumedusoid, but as a living entity.

Once the medusa is released from its hydroid it begins an independent existence which may last for a few hours while it becomes sexually mature (as in *Podocoryne carnea*) or as in the majority of medusae it may live for weeks and even months in the plankton. The typical planktonic medusa may be released at a small size of about 1mm. in bell-height and possess one to four tentacles. It grows by feeding on the zooplankton and many species have their own fishing technique when using their tentacles for capturing prey. In due course some medusae (according to species) may possess about 150 tentacles and have a bell height greater than 30 mm. but the majority do not attain this size. It may have a characteristic form of gonad, bud daughter medusae, and its eggs may or may not enjoy some measure of brood protection. During all this time too it may exhibit a certain pattern of behaviour and may have its own characteristic kind of diurnal vertical migration.

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[1] *Coryne pusilla* Gaertner is here selected as the type species of *Syncoryna* Ehrenberg, 1834, so that this genus falls into the synonymy of *Coryne* Gaertner. *Sarsia* Lesson, 1843, thus becomes available for both hydroid and medusa of species co-generic with *Sarsia tubulosa* (M. Sars) (the type species of the genus).

All these, no less than the morphological structure of the medusa, are essential characteristics of the species, and cannot be divorced from our concept of it.

Enough has been said to demonstrate the wide gulf between the fixed gonophore and the free medusa for me to be in complete agreement with Browne's statement: "I certainly prefer to place Hydroids, like *Bougainvillia*, with planoblasts, and Hydroids, like *Bimeria*, with sporosacs into separate genera, though there may be a few cases in which it is hard to draw the line". (1907, p. 19.)

I had been influenced in some earlier papers by Kramp's arguments in his classification of *Corydendrium* in placing hydroids with fixed and free gonophores in the same genus wherever possible (but I did not subscribe to his views of maintaining separate medusa genera for the medusae of those same hydroids). More experience has convinced me that the classification of hydroids in this way is only feasible in a few well defined groups of species and that the use of separate genera is justifiable and the only suitable course for the vast majority of species in the present state of our knowledge. To avoid any possible misunderstandings, I repeat, that by separate genera, I mean separate genera for hydroids with fixed gonophores and for hydroids with free medusae, the generic name applied to the latter group being used as a common name for the hydroid and medusa of the same species, and not in the sense used by Kramp (1949, p. 188) who puts the hydroid and the medusa of the very same species into separate genera to retain an out-of-date dual classification.

The retention of appropriate genera, in accord with nomenclatorial practice in other groups of animals, for species with or without a pelagic phase will facilitate the creation of a single classification for medusae and hydroids, and at the same time it will be possible to perpetuate old established generic names like *Sarsia*, *Euphysa* and *Podocoryne*, in the medusae and *Coryne*, *Bimeria* and *Garveia* in the hydroids. No insurmountable difficulties will be encountered provided the concept of a type species for each genus is borne in mind. Thus in the Corynidae we have:

Genus.	Type Species.	Type of Gonophore.
Coryne Gaertner, 1774	*C. pusilla* Gaertner	Fixed gonophore
Sarsia Lesson, 1843	*Sarsia tubulosa* (M. Sars)	Medusa
Stauridiosarsia Mayer, 1910	*Stauridiosarsia producta* (Wright)	Medusa
Dipurena McCrady, 1857	*Dipurena strangulata* McCrady	Medusa

One of Kramp's objections to a single classification for medusae and hydroids concerns the fate of species of which only a part of the life history is known. But their place in any scheme is no different from that of similar species in the present dual classification, for their status depends solely on whether we consider them co-generic with the type species and the discovery of new facts about them may or may not necessitate minor changes in classification, such as transfer to another genus or even the creation of a new genus for them.

It has already been indicated that on the whole the generic differences established for medusae are sound ones and with minor adjustments can be merged into a single classification for the Athecate or Anthomedusan forms. There is greater diversity of form in the medusa phase and this is not surprising when we consider that the species finds fuller opportunity for expression in a free planktonic phase than in a sedentary benthic phase ; the latter often persists in a fairly simple form.

Good examples of this are found in *Cladonema radiatum* and *Dipurena* sp. Vannucci in which the hydroids belong to the basic Corynid type with an oral whorl of capitate tentacles and an aboral whorl of filiform tentacles. In the sterile condition these hydroids are identical in appearance ; their medusae however are markedly different, that of *Dipurena* being a typical Sarsiid of the family Corynidae and the other, *C. radiatum*, being so highly evolved and specialized as to require a separate family, the Cladonemidae for it (Plates 12 & 13). Similarly the hydroid *Zanclea costata* (Gegenbaur) could be included in the Corynidae on its trophosome alone but its medusa is a specialized aberrant form also necessitating the status of family rank. (Text-fig. 47).

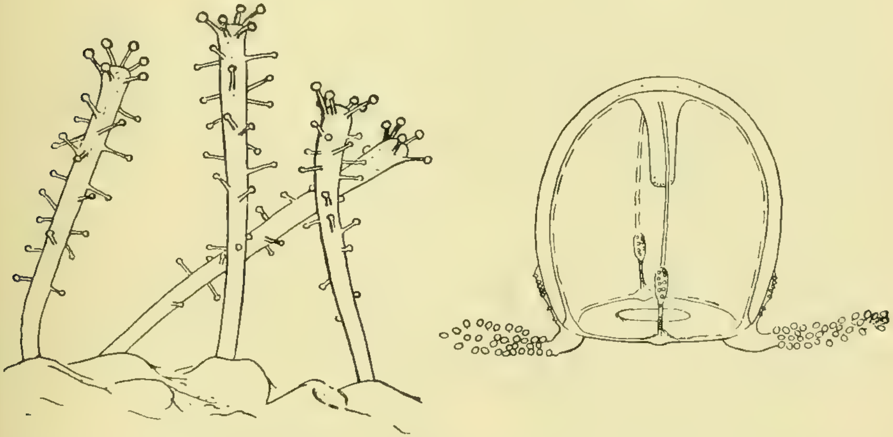

FIG. 47. *Zanclea costata* Gegenbaur : hydroid and medusa (after Russell & Rees, 1936).

Clavatella prolifera Hincks, now more accurately known as *Eleutheria dichotoma* Quatrefages, achieves family rank on the aberrant nature of its crawling medusa but the hydroid looks like a Corynid in which all the tentacles except the oral whorl have disappeared. (Text-fig. 48).

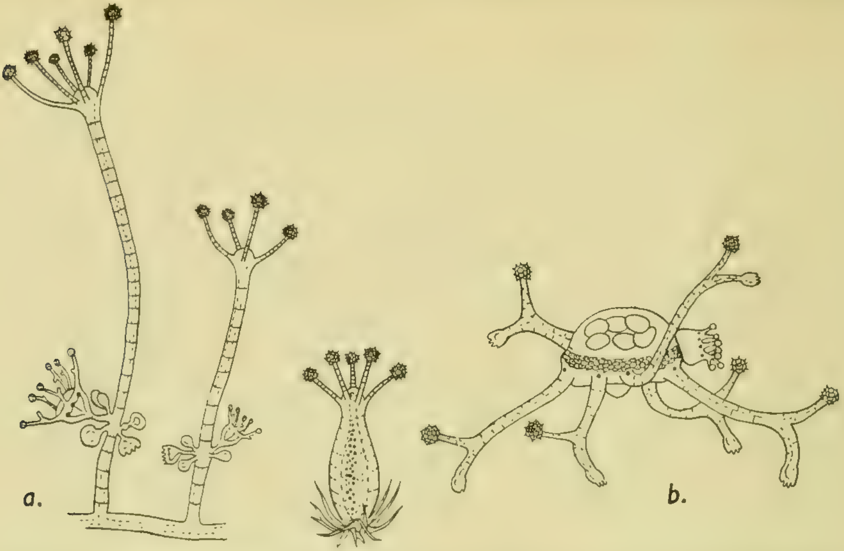

FIG. 48. *Eleutheria dichotoma* Quatrefages: A, hydroid with medusa buds (after Hincks, 1861); B, medusa (redrawn from Russell, 1953).

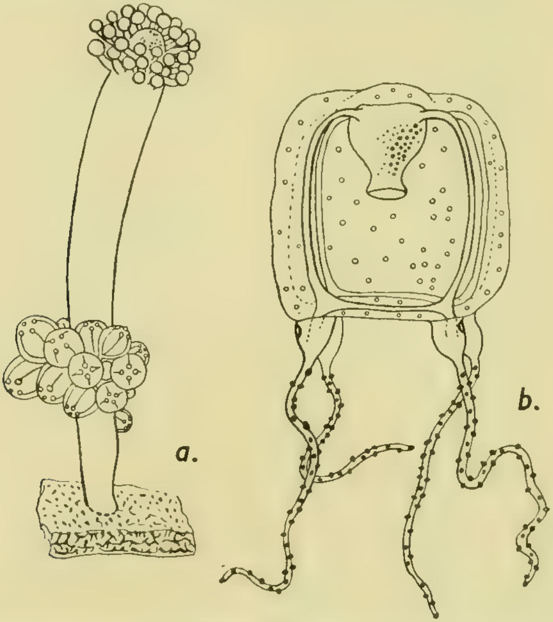

FIG. 49. *Hydrocoryne miurensis* Stechow: A, hydranth with encrusting base (redrawn after Stechow, 1909); B, newly liberated medusa (redrawn from Uchida, 1932).

In *Hydrocoryne* it is the hydroid which has evolved most (Text-fig. 49). The mesogloea has thickened to become the forerunner of a skeletal formation. There is an encrusting base. Here then the hydroid has made considerable progress towards the development of a skeleton but it is noteworthy that its medusa has remained essentially Sarsiid in character. (Text-fig. 49*b*).

Hydrocoryne and *Eleutheria* have similar polyps in which there is a single whorl of capitate tentacles around the mouth, and, although they appear to have diverged early, seem to have a common ancestor. *Cladonema*, too, seems to have some affinity with *Eleutheria* but here also they have evolved along different lines. The feature of immediate interest is the presence of armed mouth lips in the medusa—this together with the form of the polyp in *Hydrocoryne* and *Eleutheria* suggests that the Hydractiniidae arose from the same common ancestor as these three forms. It should however be noted that no significance is attached to the presence of encrusting bases in both *Hydrocoryne* and *Hydractinia* as these features appear to have arisen in different ways.

In the higher Filifera the hydroid is reduced to the simplest form of nutritive polyp and often the nature of the gonophore is the only means of distinguishing species for certain. Thus in *Stomotoca* (i.e., *Amphinema*) the two British species, almost indistinguishable on trophosome alone, can readily be identified by the newly liberated medusa (Rees and Russell, 1937). Similarly the same holds true for *Bougainvillia ramosa* and *B. superciliaris* hydroids.

The gonophore is thus of paramount importance for recognizing many species and hydroid specialists sometimes commit serious errors in classification through ignoring the diagnostic features of the medusa phase. In this way, Vervoort (1946*a*) placed *Bimeria* in *Leuckartiara* as a subgenus without realizing that its relationships were with the Bougainvilliidae and not in the Pandeidae where he had assigned it. Consideration of other Bimerid hydroids, which also have the bases of the tentacles of the hydranth clothed in perisarcal tubes (as in *B. vestita*), reveals that they have Thamnostomid medusae and that their real affinities are with the Bougainvilliidae.

There are only a few instances known in which the free medusae are alike and practically indistinguishable and the hydroids are different. The best known example is *Stauridiosarsia producta* whose medusa is indistinguishable from *Sarsia eximia* but differences have been noted in the hydroids. In the *S. producta* hydroid there is a whorl of filiform tentacles and the capitate tentacles have a tendency to be arranged in whorls, while the *S. eximia* hydroid is a typical Corynid. These differences tend to be obliterated however in older colonies of *Stauridiosarsia* for the filiform tentacles may disappear and the capitate tentacles become scattered. There is a suggestion here that we may be dealing with growth stages of the same species, but this requires careful study (see also pages 462–463).

In the Thecata there are no certain means of recognizing the adult medusae of the hydroids described as *Clytia johnstoni*, *C. gracilis* and *C. pelagica* and the medusae now go under the name *Phialidium hemisphaericum* (L.). Similarly it is possible to recognize three forms of *Obelia* hydroid, viz.: *O. geniculata*, *O. dichotoma* and *O.*

longissima but it is not possible to recognize three species of medusa of this genus in the plankton in the areas in which they occur. (Russell, 1953, p. 297).

These few examples however are not typical of the group and in general the medusae are a most useful means of recognizing evolution to specific, generic and even family rank among hydroids which have differentiated but little, or have even become reduced, as regards the trophosome.

8. THEORIES ON THE ORIGIN OF THE ALTERNATION OF GENERATIONS

There are three main theories of the origin of the curious life cycle of hydroids and medusae, viz.: the hydroid theory, the actinula theory and the medusa theory. Of these the second and third are complementary and are the more acceptable to recent workers although the first has some supporters.

1. *The hydroid theory*

For a long time the generally accepted view of the alternation of generations in the Hydrozoa was that the medusa was simply either a reproductive organ or sexual zooid, which, by a process of evolution, had become free for the better dispersal of the reproductive cells (Huxley, 1877). This view that the species was originally represented by the hydroid was also accepted by Gegenbaur (1854, 1878) and Balfour (1880) who thought that the medusa came about by a division of labour and that it was a sexual zooid which had evolved into a free form. They explained the presence of fixed gonophores by assuming that, due to some external causes, some medusae ceased to be liberated and became degenerate. This is broadly also the view of Hamann (1890) who regarded the hydroid as the more primitive and earlier form.

This theory, sometimes called the division of labour theory, was outlined by Leuckart (1851) and elaborated by Grobben (1882). Kramp (1943) states the case as follows : " According to this theory the primary form was a fixed solitary polyp with sexual propagation ; it attained the power of vegetative propagation and the formation of colonies, and later on a division of labour was constituted, the power of asexual and sexual propagation being assigned to different individuals ; the sexual individuals detached themselves, became free swimming, and were specialized into medusae. According to Grobben the development further proceeded in two different directions : (1) the medusae were reduced to fixed gonophores, as we know them in numerous hydroids ; (2) the polypoid form was obliterated, and thus the Trachy and Narcomedusae arose ".

Kramp agrees with much of this theory but does not think it can be applied to the Trachylina. He concludes that " the polypoid ancestor of the hydrozoa was first split into a pelagic and a fixed form (I have no opinion as to which of them was the primary form) . . . The Trachylina were developed from the pelagic polypoid progenitor in accordance with the actinula theory (see p. 503) ; the Leptolian were derived from the fixed form in accordance with the theory of the division of labour, and thus their special form of metagenesis arose ". In his paper Kramp appears to be laying too much stress on the so-called polypoid gonophores of

Corydendrium dispar and on the series of generations which he describes from various hydroid colonies. These " generations " are the logical outcome of the adoption of a colonial habit and the resulting division of labour which set in ; they are, of course, descended from fixed polyps but are the latter descended from an actinuloid (Kramp's polypoid ancestor) or was the descent from the actinula of some early medusa? None of the arguments brought forward can dispel the suspicion that the first fixed polyps already possessed a medusa stage ; these other views are discussed below.

2. *The actinula theory*

It was Böhm (1878) who first raised doubts about the hydroid origin of the Hydrozoa by demonstrating that there were difficulties in accepting this view, and suggested that a planktonic actinula was the ancestor of both the fixed hydroid and the free swimming medusa. Claus (1880) comes to the conclusion that the hydroid is the larva and the medusa the adult phase and attributes the origin of the hydroid phase to asexual reproduction in the larva.

This view was elaborated by Brooks (1886) who had independently reached the same conclusion as Böhm and Claus from the study of the life cycle of medusae. Böhm thought that the ancestor might be an intermediate form and suggested that the actinula of *Tubularia* might represent the persistent retention of a planktonic ancestral phase. The discovery that the Trachymedusae have a direct development with an actinuloid larva (Metschnikoff, 1874 ; Brooks, 1886) gave much support to this idea which Brooks elaborated into what he called the actinula theory as follows :

" The view which I believe to be the true one is that the remote ancestor of the hydromedusae was a solitary swimming hydra, or actinula, with no medusa stage, but probably with the power to multiply by budding. I believe that this pelagic animal gradually became more and more highly organized and more perfectly adapted for a swimming life, until it finally became converted into a medusa with a swimming bell and sense organs, developing directly from the egg without alternation, but exhibiting during its growth the stages through which it had passed during its evolution. After this stage of development had been reached, I believe that the larvae derived some advantage from attachment to other bodies, either as a parasite within other medusae, or as what may perhaps be called a semi-parasite, upon other floating bodies such as the fronds of algae ; and that it multiplied asexually in this sessile condition, giving rise to other larvae like itself, all of which became medusae. "

" I believe that the sessile or attached mode of life of the larvae proved so advantageous to the species, that it was perpetuated by natural selection, and that the primary larva then gradually lost its tendency to become a medusa, but remained a sessile hydra, giving birth by budding to other larvae which became sexual medusae and that the medusa characteristics of these secondary larvae were accelerated, and that the primary larvae gradually acquired, at the same time, the power to produce other larvae which remained permanently, like itself, in the hydra-stage ; that in this way the sessile hydra-communities became polymorphic by division of labour, and that the sessile habit proved so advantageous that the free medusae became degraded into medusa-buds, or sexual buds on the bodies of the sessile hydras or on the blastostyles."

As already mentioned, Claus (1880) came to the conclusion that the hydroid is the larva and that the medusa is the adult and attributes the origin of the hydroid phase to asexual reproduction in the larva.

Kühn (1913) adheres to this idea believing that the ancestral hydroid must have come from a fully developed medusa with a simple hydroid phase, in other words, the kind of life cycle we find in many Trachylina. The simplest trachylines have a direct development (fertilized egg-actinula-medusa), but in some Narcomedusae we find that the actinula larva is parasitic on other medusae and may bud off other larvae, and all (including the original one) develop into medusae. A further advance is seen in *Cunoctantha parasitica* where " the parasitic larva is transformed into a sausage-shaped body, from the surface of which a large number of medusae are developed by budding " (Kramp, 1943, p. 27).

Libbie Hyman (1940, p. 635), too, supports the theory that " the ancestral coelenterate was a primitive medusa " and links this with the actinula theory and it may be added that the two theories are complementary.

As a primitive group of Hydrozoa, the Capitata might be expected to furnish some evidence concerning its origins ; this it does to some extent.

The actinula persists in the more primitive families : Tubulariidae (the hydroid *Tubularia*, the medusae of *Ectopleura dumortieri* and *Hybocodon prolifer*), Margelopsidae (the medusae of *Margelopsis haeckeli* and *Climacocodon ikari*) and in the Myriothelidae (in the hydroid *Arum cocksi* Vigurs). (Text-fig. 50). All the above are solitary forms, but an actinula is known in the colonial hydroid *Actigia pusilla* (van Beneden) of the family Corynidae.

There are also polyp or hydranth buds of a distinctly actinuloid appearance in the hydroid *Euphysa aurata*, in *Tricyclusa singularis* and in the hydroid of the medusa *Sarsia tubulosa* (*Coryne sarsii* Lovén) (Text-fig. 51). Mention must also be made of budding from the hydranth in many hydroids of the Order Limnomedusae. Can these polyp-buds also be persistent survivals indicating that the ancestral actinuloid reproduced itself by asexual budding?

There are exumbrellar nematocyst tracks of a simple kind in the medusae *Ectopleura* and *Hybocodon* (in the Capitata) and in a slightly modified form in the Filifera in *Pandea*, *Neoturris* and *Leuckartiara* (Ranson, 1937), and so far as I know no one has commented on their possible origin. It is possible that they arose originally during the development of the medusa direct from an actinula, and that as the metamorphosis took place, some of the nematocysts of the larval tentacles were left behind on the surface as the tentacles grew further and further away from the aboral end of the actinula. On this interpretation then, the perradial nematocyst tracks in Tubularian medusae have persisted from the time their ancestors had a direct development. If we accept the view that the anchoring filaments of the primitive Corymorphine are modified tentacles, this may be regarded as additional evidence in favour of the actinula-medusa theory.

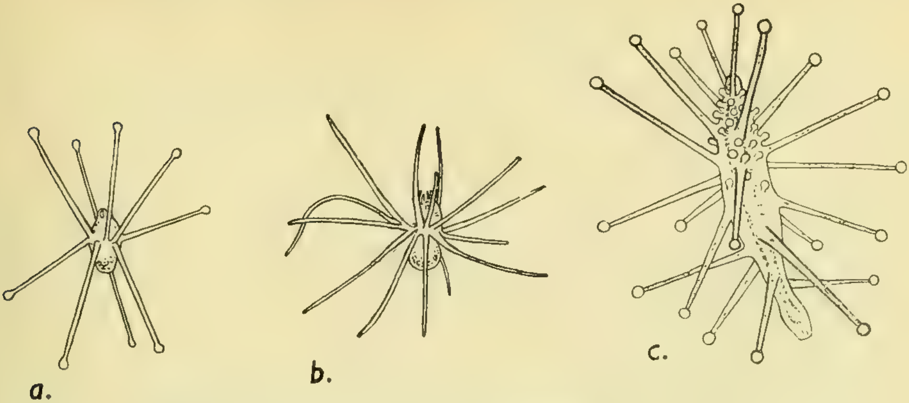

Fig. 50. Actinulae of capitate hydroids. A, *Tubularia* (redrawn from Pyefinch & Downing, 1949), B, *Hybocodon prolifer* (redrawn from Uchida, 1927), C, *Arum cocksi* (Vigurs) (redrawn from Allman, 1875).

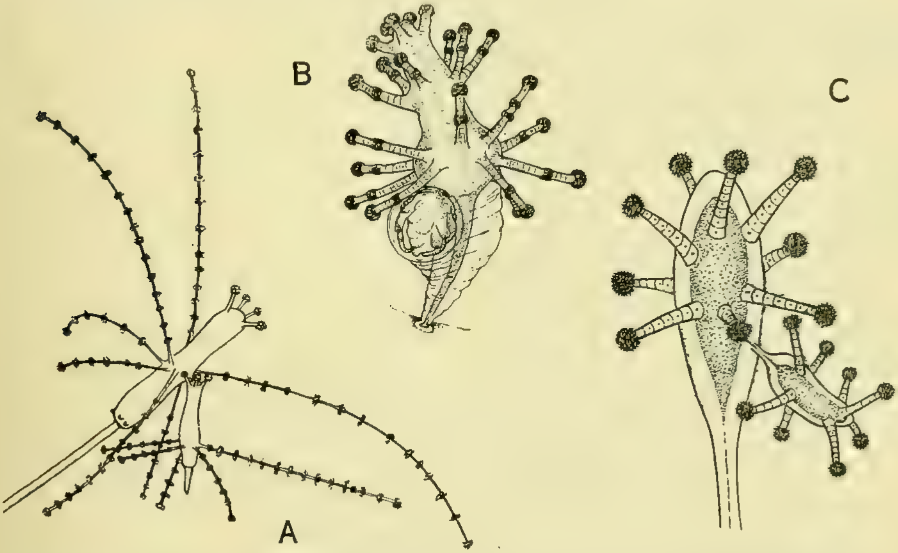

Fig. 51. Polyp-buds in capitate hydroids: A, reversed bud in *Euphysa aurata* (after Rees, 1937*b*); B, ordinary budding in *Tricyclusa singularis* (Schulze) (redrawn from Oppenheim's sketches in the Zoological Museum, Amsterdam)[1], C, polyp budding in the hydroid of *Sarsia tubulosa* (M. Sars) (after Rees, 1941).

As regards the Capitata it is reasonable to assume that their immediate ancestors already possessed a hydroid and a medusa phase, but the actinula-medusa theory harmonizes more closely with what we already know of their origins.

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[1] By courtesy of Dr. W. S. S. van der Feen.

In this review the relationships of the Capitata with some members of the Limnomedusae have not been considered for I have no personal experience of working on any of them. It seems however, that forms like *Annulella* and *Ostroumovia* have affinities with the Codonids.

9. MOSAIC PATTERNS AND RELATIONSHIPS

(a) *Mosaic patterns*

As de Beer (1954, p. 10) has stated : " It has long been held by palaeontologists that different parts of organisms are capable of independent evolution, proceeding at different rates ". Thus we have in one and the same organism a mosaic of both primitive and specialized characters as demonstrated by Watson (1919 and 1951) in *Seymouria* and *Trimerorhachis* and again by de Beer in *Archaeopteryx*.

In hydroids and medusae I have noticed when considering the sum of the characters of the hydroid and the medusa of the same species that " The result is frequently a mosaic, a blending of characteristics into a pattern which gives a much better picture of the position of the living species than does consideration of only a part of its life history " (Rees, 1956*a*). In these forms where the two phases of the life history live almost independent existences, it seems easy for them to evolve independently and for each to acquire new characteristics which are not apparent in the morphology of the other.

It is only when we recognize that these hydroids and medusae form mosaic patterns that we begin to have an understanding of possible lines of evolution within the group, and each species has to be assessed not only as I have indicated above, but also against the general picture of evolution in the class as a whole. Only in this way can we reach a rational classification with some relation to phylogeny. There are many excellent examples of mosaic evolution in the Capitata and a brief survey of some key species will help to a better understanding of relationships.

As has been apparent from the earlier part of this paper, I am inclined to the view that the Hydrozoa are medusoid in origin and that the hydroid phase is a later development. Once established however the hydroid phase has become the dominant one to the exclusion of the medusa phase in the most advanced hydroids of the Haleciidae, the Sertulariidae and the Plumulariidae. This trend towards elimination of the medusa phase is apparent however at all levels of hydroid evolution so that even in the most primitive hydroids like *Hypolytus peregrinus* and *Euphysa aurata*, we find that the one has styloid gonophores and the other a free medusa and as regards this particular feature the former may be regarded as the more highly evolved.

The characteristics of the important species in the Capitata have been brought together in the series of mosaic patterns below ; they will serve as an introduction to the discussion of relationships which follows.

The first eleven species considered below are solitary forms.

Hypolytus peregrinus Murbach

This is the simplest type of Corymorphine hydroid known to us and is probably the most primitive of Capitate hydroids (Text-fig. 4). It has two whorls of moniliform tentacles, and a soft, poorly chitinized sheath secured to the bottom by anchoring filaments. This tube can be abandoned and a new one secreted. There is no diaphragm in the hydranth and no canals in the stem. All these are primitive features but the possession of fixed styloid gonophores is a specialized feature.

Euphysa aurata Forbes

This hydroid has the same primitive features found in *Hypolytus peregrinus* but the oral tentacles have become shortened to a single terminal knob (Text-fig. 5).

The medusa has the primitive moniliform tentacle of the same type as is found in the hydroid. The ring gonad and simple mouth are characteristic Codonid features. The medusa is specialized in having lost all but one of the perradial tentacles. It is not certain whether the absence of perradial nematocyst streaks on the exumbrella means that they have been lost (Text-fig. 44, p. 492).

Boreohydra simplex Westblad

This Corymorphine is primitive in the absence of a diaphragm in the hydranth but is specialized in the complete reduction of the aboral tentacles, the partial reduction of the oral tentacles and in the reduction of the gonophores to cryptomedusoids (Text-fig. 52). The stem, too, is solid and highly muscular.

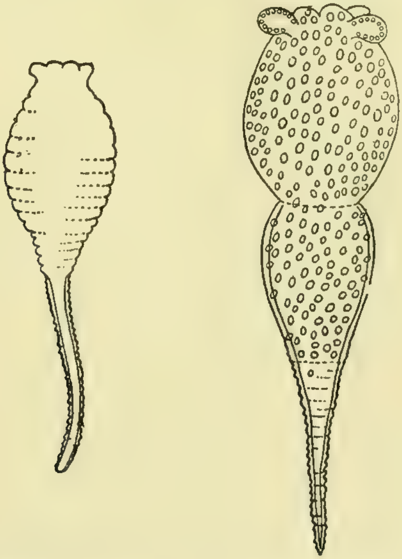

FIG. 52. *Boreohydra simplex* Westblad : a Corymorphine hydroid in which the aboral tentacles have been lost.

Corymorpha nutans M. Sars

Of the solitary hydroids this is one of the more highly evolved in the large size and elaboration of the individual polyp (Text-figs. 7 and 12). The medusa has evolved but little and is very similar to that in *Euphysa aurata* (a much simpler hydroid).

Features which may be regarded as related to size are: the large number of tentacles in the oral and aboral sets of tentacles, the parenchymatous cushion and diaphragm for the support of the aboral whorl of tentacles, proliferation of the budding area into long hollow branched blastostyles, parenchyma in the stem and the formation of stem canals, a large number of filaments and a more adherent perisarc resulting from a stiffening of the stem.

Apart from changes related to size this species is more advanced than *Euphysa aurata* in its filiform tentacles, but the larval hydroid still has capitate oral tentacles.

Tricyclusa singularis (Schulze)

This aberrant solitary hydroid is primitive in the possession of a gelatinous sheath-like stem perisarc, there appears to be no diaphragm and the oral tentacles are capitate (Text-fig. 6, p. 462).

This species has the above features in common with a possible *Euphysa*-like ancestor, but is specialized in the following characteristics: The interpolation of an additional whorl of tentacles, a reduced moniliform arrangement of nematocysts on the intermediate and aboral whorls of tentacles, a basal disk for attachment of the hydroid to the substratum and the reduction of the gonophores to cryptomedusoids.

Margelopsis haeckeli Hartlaub

Margelopsis haeckeli is one of the few pelagic species of Capitate hydroids (Text-fig. 31, p. 482). There is no stem, only an invagination with vacuolated cells. The hydranth conforms in external morphology to a Tubularian with two whorls of filiform tentacles in the adult.

The medusa has the ring gonad and simple mouth on the manubrium. The eggs develop into actinulae on the manubrium and this is considered a primitive feature found mainly in the Tubulariidae and only exceptionally in colonial corynids.

The medusae of *Margelopsis* and its near relatives are unique among Codonids in having several tentacles grouped together in each perradius, and this arrangement must be regarded as a specialized feature.

Pelagohydra mirabilis Dendy

Pelagohydra must be regarded as a highly modified Margelopsid (Text-fig. 21, p. 470). Its medusa however has remained essentially Margelopsid in character.

The *Pelagohydra* polyp is specialized in the following features: (1) The enormous development of the parenchyma of the diaphragm resulting in (2) The obliteration of the aboral chamber and much of the oral chamber with (3) The development of a peripheral canal system for feeding the tentacles and blastostyles and (4) The scattering of the aboral whorl of tentacles and also of the blastostyles.

Ectopleura dumortieri (van Beneden)

The *Ectopleura* hydroid, like *Tubularia*, has a firm adherent perisarc and the tentacles are all filiform in the adult; that is, it has progressed beyond the Corymorphine stages.

Its medusa has a much modified arrangement of the nematocysts on the tentacles, obviously derived however from the moniliform type, but in other respects, it is an ordinary Codonid medusa with ring gonad and simple mouth. In its possession of four perradial tentacles, and the exumbrellar nematocyst streaks, it is possibly more primitive than typical *Corymorpha* and *Euphysa* medusae (Text-fig. 41, p. 491).

Acaulis primarius Stimpson

Acaulis primarius retains the simple gelatinous tube and the filaments of the lower Corymorphine. It has, however, transformed its aboral whorl into thick, fleshy, filiform tentacles, and has developed scattered capitate tentacles in the intertentacular area (Text-fig. 13, p. 466). Its ancestor must have been an unspecialized Corymorphine which had lost the moniliform arrangement of the nematocysts but retained the gelatinous tube and the anchoring filaments. *Acaulis* has fixed gonophores.

Monocoryne gigantea (Bonnevie)

Monocoryne is a rather specialized species but it has retained a few stout anchoring filaments (Text-fig. 38, p. 488). Here the gelatinous tube has become a firm perisarc, the scattered capitate body tentacles of *Acaulis* have become fused in groups of three to form trifid (sometimes quadrifid) tentacles and the fixed gonophores are hermaphroditic.

Arum cocksi Vigurs

This Myriotheline hydroid (the *Myriothela phrygia* of Hincks) is possibly the most highly specialized solitary hydroid known (Text-fig. 15, p. 467). It has a simple lamellar perisarc at the base with modified anchoring filaments. In other respects, viz.: its numerous body tentacles, its branched coryniform blastostyles, its special claspers for the fertilized egg, the highly organized actinuloid larva and its ridged endoderm, it is highly specialized.

The related *Myriothela phrygia* (Fabricius) is notable for the absence of perisarc and for its retention of the anchoring filaments in a slightly modified form.

Asyncoryne ryniensis Warren

This is a colonial hydroid with a creeping stolon and a firm perisarc. In other respects the hydroid is rather primitive. Its hydranth suggests that it has evolved direct from the lower Corymorphines; it has an oral whorl of capitate tentacles and has retained the moniliform type of aboral tentacle. These, however, have become scattered over the body of the hydranth. Gonophores are fixed.

The structure of the hydranth, particularly the retention of the moniliform tentacle, indicates that this species has evolved along a different line from other corynoid hydroids (Text-fig. 3, p. 459).

Halocordyle tiarella (Ayres)

Halocordyle, better known as *Pennaria*, has an exceptionally well developed, upright, branched hydrocaulus with regular branching and possessing ringed perisarc at the origins of branches (Text-fig. 25, p. 474). As regards this feature it is more advanced than any member of the related family Corynidae.

Its hydranth is however little removed from the basic type of Corymorphine and its ancestor might well have been something rather like the larval *Corymorpha nutans*, the only essential difference in external morphology of the hydranth being the addition of scattered capitate tentacles between the oral capitate whorl and the aboral filiform whorl (Text-fig. 53). In the latter these aboral filiform tentacles are fully developed and are not reduced in any way.

The fully developed medusa is without tentacles and is seldom freed. Its structure is essentially Codonid.

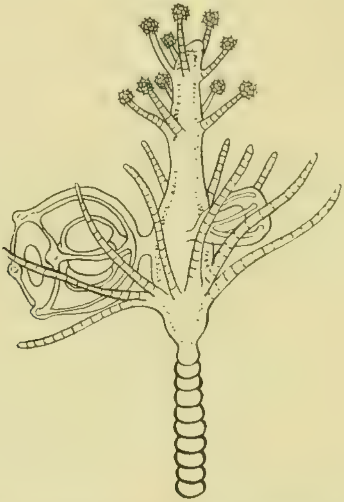

FIG. 53. *Halocordyle tiarella* (Ayres) with female medusa bud still attached (redrawn from Mayer, 1910).

Stauridiosarsia producta (Wright)

In this colonial Corynid there is a creeping stolon but the upright hydrocaulus is poorly developed. Here the hydranth has an oral whorl of capitate tentacles, scattered capitate body tentacles and a reduced whorl of aboral filiform tentacles (Text-fig. 10). These reduced filiform tentacles reflect the trend in the Corynidae where the filiform tentacles are lost (see p. 462).

The medusa has four radial canals, four perradial marginal tentacles, a ring gonad and simple mouth. All these are primitive features, and, together with the ocellus on each tentacle, are typical of Sarsiid medusae. The tentacles of this and other species of corynid medusae reflect the varying degrees to which the ancestral moniliform condition of nematocyst armature has been reduced.

Cladocoryne floccosa Rotch

Cladocoryne is primitive in having an unbranched hydrocaulus and in the large size of its hydranth (Text-fig. 54). In other respects it is rather specialized, especially in its scattered coryniform tentacles. The origins of this form are obscure but it may have arisen from an unspecialized Acauloid stock where the tendency to develop coryniform tentacles may be noted in *Monocoryne* (where there are trifid capitate tentacles) and in the so-called blastostyles of *Arum cocksi*.

Cladocoryne has fixed gonophores borne on the body of the hydranth.

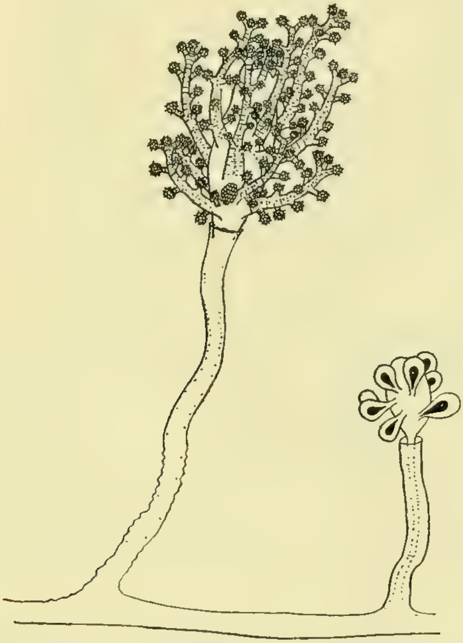

FIG. 54. *Cladocoryne floccosa* Rotch: two hydranths, one sterile and one reduced to a blastostyle (redrawn from du Plessis, 1881).

Cladonema radiatum Dujardin

The hydroid has a creeping stolon but an upright hydrocaulus is not developed. The hydranth retains all the essential features of a larval *Corymorpha*—an oral whorl of capitate tentacles and an aboral whorl of filiform ones. Medusa buds continue to be borne in the intertentacular area. All these are primitive characteristics.

The medusa retains certain primitive features, viz.: the Sarsiid ocellus and the continuous ring gonad. In other respects the medusa is highly specialized. There are 4–11 radial canals and a corresponding number of tentacles; the latter are coryniform with 1–4 stalked adhesive organs. The mouth has 4–5 lobes each armed with a nematocyst cluster.

This species is a good example of a very specialized medusa with a simple, little-changed hydroid (Plates 12 & 13).

Eleutheria dichotoma Quatrefages

In *Eleutheria dichotoma* (the hydroid was described by Hincks as *Clavatella prolifera*) the polyps arise from a creeping stolon; they are long and possess only an oral whorl of capitate tentacles, the aboral whorl being missing. In these characters the hydroid is simplified, but the medusa buds have moved down nearly to the base of the polyp away from the digestive area (Text-fig. 48, page 500).

The medusa is highly specialized and adapted to a creeping habit instead of a planktonic one. It has, however, retained the simple mouth and the Sarsiid ocellus. There are more than four radial canals and a corresponding number of tentacles; the latter are branched once and have an adhesive organ at the tip of one and a capitate head at the other. The gonads are in a special brood pouch situated above the stomach.

As in *Cladonema*, *Eleutheria* has a fairly simple hydroid and a much modified medusa.

Hydrocoryne miurensis Stechow

Hydrocoryne miurensis has the same simplified type of hydranth as *Eleutheria* but is rather specialized in the possession of a thickened gelatinous, ridged mesogloea in the hydranth and in the possession of an encrusting base with the same mesogloeal thickening.

Its medusa has four radial canals, a ring gonad and four tentacles exhibiting traces of the moniliform arrangement of nematocysts. Here then the hydroid is much modified and the medusa retains the basic features of the Corynid medusa (Text-fig. 49, page 500).

Zanclea costata Gegenbaur

In this hydroid the polyps are typical Corynids without filiform tentacles (Text-fig. 47, page 499). The gonophores are borne on the hydranths and the latter may become reduced to complete blastostyles. There is however some indication that division of labour is setting in and that some polyps are less likely to bear gonophores than others.

The medusa retains the simple mouth, the four radial canals and the four tentacles of the Codonid. It has however many specialized features: the tentacles have numerous stalked abaxial capsules containing nematocysts, the exumbrellar nematocyst armature is confined to special tissue, the ocelli have been lost and the gonad is split up into four interradial groups.

Rosalinda williami Totton

As in *Zanclea* the hydranth is typically corynid with numerous scattered capitate tentacles. The chief interest of the species lies in the fact that it has an encrusting base from which the hydranths arise. This encrusting base is believed to have an internal mesogloeal skeleton as in the Solanderiidae.

The reproduction of this species is not known.

Dendrocoryne misakinensis Inaba

The simple Corynid hydranth is found here also but in other respects this species is one of the most advanced Capitate hydroids. There is an upright, branched gelatinous skeleton completely covered in ectoderm. The gonophores are not borne on the hydranths but on the rhizocaulome formation.

Ptilocodium repens Coward

This is an aberrant form found on the leaves of the pennatulid *Pennatula fimbriata* Herklots. The gonophores are borne at the base of the hydranth and are fixed eumedusoids with four radial canals and a ring gonad (Text-fig. 55).

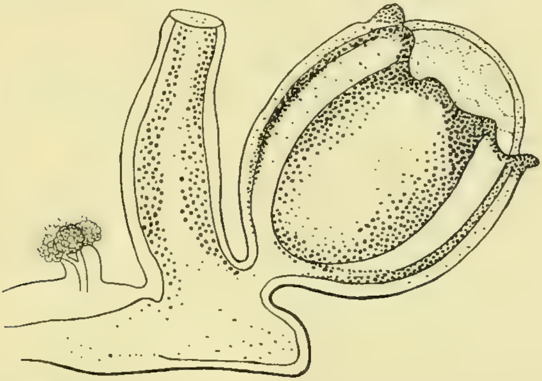

FIG. 55. *Ptilocodium repens* Coward, an aberrant Corynoid with a nutritive zooid and a dactylozooid (redrawn from Leloup, 1940).

The specialized features are many: the coenosarc is naked and encrusting, the sessile nutritive polyps have no tentacles, and there are sessile dactylozooids with four short capitate tentacles.

This species is insufficiently known but it may have a common origin with the ancestors of *Millepora*. Another interesting feature is the division of labour in the polyps, the one concerned with feeding and reproduction and the other with protection.

(b) *Relationships*

The division of the athecate hydroids into Capitata and Filifera by Kühn (1913) was a great advance on earlier classifications, and, if we omit species later removed to the Limnomedusae, these two divisions (the one with capitate tentacles in the hydroid and a ring gonad in the medusa, and the other with filiform tentacles in the hydroid and a non-Codonid medusa) form natural groups which can be applied both to the hydroid and the medusa phases.

Kühn thought that the Corynidae were the most primitive Codonids and proceeded to derive the other families from them, and this is the scheme which has been in use ever since. Both Kramp (1949) and Russell (1953) have accepted the Corynidae as the most primitive family of capitate forms. Ample evidence has been brought forward here to demonstrate that on general principles the Corynidae as colonial animals are secondarily simplified, and I am in agreement with Totton (1954) that to derive solitary forms like *Tubularia* and *Corymorpha* from colonial ones is " most improbable ".

The solitary forms are more primitive than the colonial forms for reasons already given and it is among these that we have to look for forms resembling the ancestral capitate hydroid. The lower Corymorphines *Euphysa* and *Hypolytus* retain many ancestral features and in all essentials could be the starting point for capitate evolution (Figs. 56–58).

From this type of hydroid may be traced three primary lines of evolution: (1) The *Tricyclusa* line represented by one species so aberrant that a new superfamily is justifiably created for it. (2) The *Asyncoryne* line represented by one species which has become colonial. (3) The higher forms including the colonial Capitata, the Tubularians and the *Acaulis-Myriothela* group (discussed further below).

The lower Corymorphines seem to have given rise to an unspecialized *Corymorpha* in which the oral capitate tentacles were retained and the aboral tentacles had become filiform. This must have been rather like the larval *Corymorpha nutans* and can be regarded as a basic type from which all other Capitate hydroids arose.

This basic type of hydroid appears to have evolved in three different ways to give rise to: (1) The *Corymorpha–Tubularia–Margelopsis* line, all essentially solitary forms; (2) The *Acaulis–Myriothela* line of solitary hydroids; (3) The colonial Corynoidea (except the Asyncorynidae and the Cladocorynidae).

These form three main groups which are raised to the rank of superfamilies in recognition of the separate, distinctive, evolutionary trends they display.

The *Tubularia* line, as the first may be called, arose from the lowly Corymorphine evolving filiform tentacles in the adult and a more or less complete diaphragm. From this the Tubulariidae may be assumed to have arisen through the evolution of a firm perisarc, loss of anchoring filaments with settlement of the larva on a firm substratum, together with partial atrophy of the diaphragm and the stem canals to form a sieve plate. *Branchiocerianthus*, too, as has already been explained, is unintelligible without a Corymorphine ancestry (p. 472).

The Margelopsidae, also, although aberrant pelagic forms, seem to have Tubularian affinities although the medusa has evolved along its own lines. In *Pelagohydra* as has been noted (p. 471) the diaphragm has become the float but not enough is known of the *Margelopsis* hydroid to estimate whether the diaphragm was present and has become reduced.

The *Acaulis–Myriothela* line stands on its own as a group of solitary hydroids. *Acaulis* is little removed from the basic type of Corymorphine with its gelatinous tube and filaments. This noticeable failure to develop a firm upright hydrocaulus and the tendency for the animals to become long and vermiform are characteristics of the group as a whole. Apart from the multiplication of capitate tentacles in the intertentacular area, there is a tendency towards the development of coryniform tentacles (trifid in *Monocoryne* and both simple and coryniform ones in *Arum cocksi* where the latter carry the gonophores).

The colonial Capitata classified here as the Corynoidea includes nearly all those species which I am inclined to think arose from a form like the larval *Corymorpha*, but two families, the Asyncorynidae and the Cladocorynidae (included in this superfamily because they are colonial forms) seem to have originated in a different way. The affinities of the former with the most primitive Corymorphines has already been noted but the Cladocorynidae may have arisen from early Acauloid stock where the tendency to produce a coryniform tentacle has already been indicated. Their position in this superfamily is, of course, tentative, but to include them in other or new superfamilies would not be justified at present for we do not know enough about the two species on which the families are founded. Picard (1955) places *Cladocoryne floccosa* Rotch in the Pteronematidae (Zancleidae of this report), but does not give sufficient reasons for the acceptance of his view here.

The morphology of the simpler Corynoid polyps is very little removed from the larval *Corymorpha* but they have become colonial with creeping stolons and rudimentary hydrocauli. Such polyps are found in *Cladonema*, *Dipurena* sp. (Vannucci 1956, in press) and in the larval *Stauridiosarsia*. The typical Corynids differ little from this basic type except in the disappearance of the filiform tentacles (persisting in some species as " false " tentacles) and the development of additional intertentacular capitate tentacles. The medusae differ but little from the basic type but each tentacle base has developed an ocellus. We see, too, the breaking up of the regular moniliform arrangement of the tentacular nematocysts.

The Halocordylidae seem to have branched off quite early from the Corynoid stem and have retained the filiform tentacles without reduction (as opposed to the Corynid line where they have become progressively reduced and even lost) and have acquired additional intertentacular capitate tentacles on the hydranth. These together with an exceptionally well developed, branched hydrocaulus, are the chief features of Halocordylid evolution.

The Cladonemidae, the Eleutheriidae and the Hydrocorynidae seem to have arisen from the common Corynoid stock which also gave rise to the Corynidae and the Halocordylidae. The Hydrocorynidae soon evolved along a line whose chief characteristics were the loss of the filiform tentacles, the fusion of the basal stolons to form an encrusting base and the development of a thick gelatinous mesogloeal skeleton. At the same time the medusa (when young at least) retained features which are essentially Sarsiid (Text-fig. 49, p. 500). In the Eleutheriidae, too, the filiform tentacles are lost (as in some Cladonemids) but the trophosome remains simple and it is the medusa which has evolved, as already noted, for a creeping mode of life. In the Cladonemidae, also, the hydroid remains almost unchanged and in external morphology is still a simple Corynid of primitive appearance, but the highly evolved medusa has some features such as the adhesive organs and branching of the tentacles in common with that of *Eleutheria*. Although each family has been derived from a common stock they appear to have diverged early.

The Solanderiidae consist of both simple and branched forms, the one with an encrusting base and the other with an upright, branched formation. They are, as already indicated for *Dendrocoryne*, an advanced group with many specialized features but the form of the polyps (typical Corynids) suggests that they have arisen from the Corynid stock. The mesogloeal skeleton may have arisen independently in this family and in the Hydrocorynidae, but this little known group should be studied in detail in places where living material is available.

The Ptilocodiidae also requires study. All that can be said is that it belongs to an aberrant Corynoid stock which probably also gave rise to the Milleporina, but it is itself too specialized to be regarded as an ancestral stage in their evolution (Text-fig. 55).

The Zancleidae of Russell is by definition (Russell, 1953, p. 98) an assemblage of forms in which the hydroids " have irregularly distributed tentacles, either all capitate, or all filiform or of both types " but all have zancleid medusae. It thus includes the Corynipteridae Weill and the Clavipteridae Weill (1934*b*). As Russell has mentioned only one species, *Zanclea costata*, this is the type of the family and fortunately it is well known. The mosaic presented by *Zanclea* implies that it arose from a Corynid stock by considerable evolution in the medusa. It has one type of nematocyst (macrobasic eurytele) which has not so far been reported in the lower Capitata.[1] This same type of nematocyst is also found in *Pteroclava* (a species with scattered filiform tentacles and a zancleid medusa), as well as in the Chondrophore *Velella* (Picard, 1955). The mosaic in *Pteroclava* is very similar to that in *Zanclea* and there is a suggestion here that the change from capitate to filiform tentacles is fairly recent in origin.

Picard (1955) has put forward a very interesting theory that the Chondrophora (*Velella*, *Porpita* and *Porpema*) have arisen from what he calls Pteronematidae, but before discussing this theory it may be desirable to ascertain what we mean by this name to-day.

This family, the Pteronemidae, was created by Haeckel (1879) as a subfamily of Cladonemidae and included the genera *Pteronema*, *Zanclea*, *Gemmaria* (synonymous with *Zanclea*) and *Eleutheria*. Subsequently Hartlaub (1907) transferred *Eleutheria* to the Dendronemidae (another subfamily of Cladonemidae) and added *Halocharis* and *Mnestra*, the one being, and the other probably, synonymous with *Zanclea*, to the Pteronemidae. Mayer (1910) referred *Zancleopsis* Hartlaub 1907 to the family.

Subsequently the families Eleutheriidae (Russell, 1953), and Zancleidae (Russell, 1953) were set up for their respective genera so that the Pteronemidae has become

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[1] Undue significance should not be attached to the apparent absence of a macrobasic eurytele in the solitary Capitata for the nematocysts of these forms have been studied by very few workers. Sometimes a particular kind of nematocyst is found in the medusa and not the hydroid (and *vice versa*).

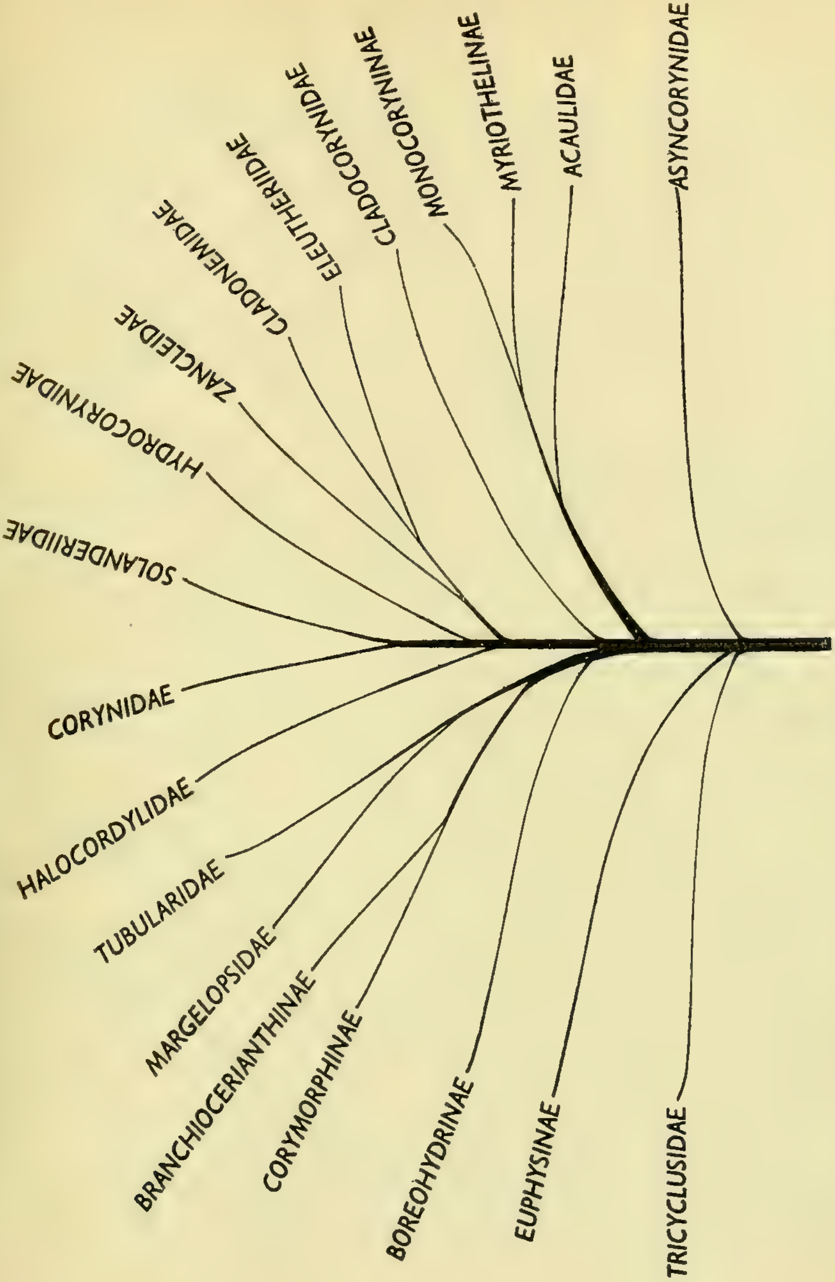
SOLANDERIIDAE
HYDROCORYNIDAE
ZANCLEIDAE
CLADONEMIDAE
ELEUTHERIIDAE
CLADOCORYNIDAE
MONOCORYNINAE
MYRIOTHELINAE
ACAULIDAE
ASYNCORYNIDAE
CORYNIDAE
HALOCORDYLIDAE
TUBULARIDAE
MARGELOPSIDAE
BRANCHIOCERIANTHINAE
CORYMORPHINAE
BOREOHYDRINAE
EUPHYSINAE
TRICYCLUSIDAE

Fig. 56. Phylogeny in capitate hydroids: a diagram showing the relationships of the families of capitate hydroids.

restricted to *Pteronema* (itself an imperfectly understood genus) and *Zancleopsis* (which obviously does not belong to the family). Reference must also be made to the Cladonemidae, which has now been restricted to *Cladonema* and closely related forms by Russell (1953), and also to the Dendronemidae Haeckel, the second of Haeckel's Cladonemid subfamilies, containing the genera *Ctenaria*, *Cladonema* and *Dendronema*. The second of these genera, the type of the Cladonemidae, has been re-classified by Russell (1953) so that *Ctenaria* and *Dendronema* are excluded from the family. We are thus left with three genera, *Pteronema*, *Ctenaria* and *Dendronema* that are too imperfectly known to justify any re-definition of the family Pteronemidae.

In his theory that the Chondrophora are of " pteronemid " origin, Picard obviously uses the name in a general way, for he specifically mentions *Zanclea*, and makes some allusions to coryniform tentacles such as we find in the hydroid *Cladocoryne* and in the *Cladonema* medusa. As arguments in favour of this theory he points out that the macrobasic eurytele is common to *Zanclea* and *Velella*, the exumbrellar nematocyst tracks are confined to special tissue both in the medusa of *Zanclea* and in the *Chrysomitra* medusa of *Velella*, the resemblance of the gonozooid of *Velella* to the fertile polyp in *Zanclea* and also points out the resemblances between the double perisarc of the *Zanclea* hydroid's hydrocaulus and the chitinized float of the Chondrophores. Picard is convinced that the Chondrophora has sufficiently strong " Pteronemid " affinities that he reduces them to the status of a family, the Chondrophoridae, to be placed next to his Pteronematidae.

I do not propose to discuss here whether the Chondrophora are evolved from pelagic tubularians, as Totton (1954) believes, or whether, as Picard suggests, that they are " pteronemid " in origin, but it is pertinent to this survey to mention that the differences which separate the Chondrophora from the Athecata (Anthomedusae) are as great as separate this group from the Thecata (Leptomedusae). For this reason, I believe the Chondrophora should have the status of an Order as maintained by Totton.

CLASSIFICATION

In the classification of the Capitata which follows, the hydroids and medusae are merged for the first time into a single coherent classification to replace the dual schemes that had prevailed so long.

The classification follows the broad evolutionary trends that have been traced in the earlier part of the report, and I think it is right that these lines should be grouped, as far as our knowledge goes, into superfamilies. I have hesitated to give superfamily rank to the Cladocorynidae and the Asyncorynidae because they are imperfectly known ; they are thus placed in the Corynoidea simply because they are colonial and not because of any supposed common ancestry (but see pp. 514–515).

Nematocysts are of some use in denoting higher taxonomic groups and they are also of use in separating different species on size differences. They are however of little use at family level and in the Capitata so few forms have been studied that it is not wise to come to general conclusions. All that can be said is that the three main types seen are stenoteles, desmonemes and atriches in that order of frequency (Table IV). As so few forms have been studied, undue significance should not be

TABLE IV.

			Haplonemes.			Heteronemes.			
	Stenoteles.	Desmonemes.	Atrichous.	Basitrichous.	Anisorhize.	Microbasic mastigophores.	Macrobasic Mastigophores.	Microbasic Euryteles.	Macrobasic Euryteles
Anthomedusae (*Athecata*)									
Corymorphidae									
Corymorpha nutans M. Sars	×	×	..	..	×	(×)	..	(×)	..
Euphysa aurata Forbes	×	..	×	..	×	..	..	..	..
Boreohydra simplex Westblad	×	×	×	..	..	..	..	..	..
Tubulariidae									
Ectopleura dumortieri (van Beneden)	×	×	..	..	×	×	..	..	..
Corynidae									
Sarsia eximia (Allmann)	×	×	..	..	..	..	..	..	..
Sarsia prolifera Forbes	×	×	..	..	..	..	..	..	..
Sarsia gemmifera Forbes	×	×	..	..	..	..	..	..	..
Syncorynide C (Weill 1934*b*, p. 433)	×	..	×	..	..	..	..	..	..
Cladonemidae									
Cladonema radiatum Dujardin	×	×	..	..	..	..	..	..	..
Eleutheriidae									
Eleutheria dichotoma Quatrefages	×	×	..	..	..	..	..	..	..
Zancleidae									
Zanclea costata Gegenbaur	×	..	×	..	..	..	..	..	×
Chondrophora									
Velella velella L.	×	..	×	..	..	..	..	..	×
Porpita mediterranea Esch.	×	..	×	..	..	..	..	..	..

attached to the fact that both *Zanclea* and *Velella velella* possess macrobasic euryteles.

Apart from the fact that this classification includes both hydroids and medusae, nearly all the medusa families defined by Russell (1953) are included without modification, for they form natural groups. The chief points of difference are the elevation of his Corymorphinae to the rank of a family (a step already taken by Kramp, 1949) and the creation of superfamilies.

As regards the earlier classifications of the hydroids, the classification now presented includes a re-distribution of many of the so-called Halocordylidae, the recognition of the Euphysinae, the creation of a sub-family for *Monocoryne gigantea*, a separate family, the Hydrocorynidae for *Hydrocoryne miurensis*, the creation of super-families, as well as bringing the hydroids into line with modern concepts in classifying their medusae.

Order ANTHOMEDUSAE (ATHECATA)

Hydroids with naked hydranths without distinct thecae. Reproductive polyps when present without gonothecae. Gonophores fixed or free medusae.

Newly liberated medusa deep bell-shaped, without statocysts and usually with swollen tentacle bases. Mature medusae with gonads always on stomach and occasionally extending for a short distance along the radial canals.

It is not possible to draw a sharp distinction between some Anthomedusan forms and those found in the Leptomedusae (Thecata) and in the Limnomedusae. There are some hydroids, particularly in the *Campanopsis* group of Haleciids, in which the hydranths are naked and there are many Leptomedusae and Limnomedusae in which there are no statocysts or other marginal sense organs in the medusa. The Limnomedusae in particular is a heterogenous assemblage of forms some of which at least seem to have Codonid affinities, or, more precisely, a common ancestry with the Capitate hydroids.

Sub-order CAPITATA Kühn, 1913

Hydroids with some tentacles capitate either in the larva or in the adult. Gonophores usually borne on the body of the hydranth. Gonads in the medusa usually forming a continuous ring round the manubrium.

This is a very well defined group and the most primitive in the Anthomedusae although there are some solitary forms which have grown large and elaborate. In some Tubularian families capitate tentacles are found only in the very young hydroid, and in some aberrant medusae like *Zanclea* and *Eleutheria* the gonads no longer form a continuous ring.

Super-family TUBULAROIDEA nov.

Hydroids usually solitary but some colonial forms occur. Hydranths with two sets of tentacles, capitate, filiform, or moniliform in type, but the aboral whorl is never capitate.

Medusae (when present) with or without exumbrellar nematocyst tracks, with stomachs not extending beyond bell margin, with simple circular mouths. Four radial canals with perradial tentacle bulbs without ocelli. Tentacles four or fewer, or grouped in perradial clusters.

This superfamily is essentially a group of solitary forms, although some species of *Tubularia* are colonial, but the colonial nature of several species of *Tubularia* is in doubt. There are many Tubularoids in which both sets of tentacles are filiform in the adult hydroid, but the oral tentacles of the very young hydroids are distinctly capitate. It includes the families Corymorphidae, the Tubularidae and the Margelopsidae. In the latter family the hydroids consist of pelagic hydranths modified for a planktonic existence ; they are thought to provide a link with the Disconanth Siphonophora.

Family CORYMORPHIDAE Allman 1872.

Hydroids solitary, with perisarc feebly developed in the form of a gelatinous perisarcal sheath. Stem with anchoring filaments. Medusae, when present, with 1–4 perradial tentacles and without exumbrellar nematocyst tracks.

Type species : *Corymorpha nutans* M. Sars, 1835.

There are four sub-families, the Euphysinae, the Corymorphinae, the Boreohydrinae and the Branchioceriantinae. The Euphysinae (suggested by Haeckel, 1879, for *Euphysa* medusae) is re-established now, to mark the wide gulf which exists between the hydroids of the lower Corymorphines (*Euphysa*, *Hypolytus* and possibly *Gymnogonos*) and the elaborate higher Corymorphines like *Corymorpha*, which have filiform tentacles, stem canals and an exceptionally well-developed diaphragm. *Branchiocerianthus* can be regarded as essentially a Corymorphine, despite its secondarily acquired bilateral symmetry, and is accordingly given the rank of a sub-family.

Sub-family EUPHYSINAE

Hydranths radially symmetrical, without diaphragm and without fully developed stem canals. Oral tentacles, capitate or moniliform, aboral tentacles moniliform. Fixed gonophores or free medusae.

Type species : *Euphysa aurata* Forbes.

Sub-family CORYMORPHINAE

Hydranths radially symmetrical, with diaphragm, and stem canals. Tentacles all filiform in the adult hydroid. Fixed gonophores or free medusae.

Sub-family BOREOHYDRINAE

Hydranths radially symmetrical, without diaphragm, with one whorl of oral capitate tentacles. Aboral whorl missing. Fixed gonophores, where known.

Type species: *Boreohydra simplex* Westblad, 1937.

There appears to be no justification for keeping *Boreohydra* in a separate family of its own as proposed by Westblad, and I propose to treat it as an aberrant Corymorphine.

Sub-family BRANCHIOCERIANTHINAE

Hydranths bilaterally symmetrical, with diaphragm, with two sets of filiform tentacles.

Fixed gonophores (where known).

Type species: *Branchiocerianthus urceolus* Mark, 1898 (Text-figs. 23–24, pp. 472–473).

Family TUBULARIIDAE Allman, 1864

Hydroids essentially solitary but with some colonial forms. Stems covered with firm perisarc. Hydranths with two whorls of filiform tentacles in the adult. Anchoring filaments very seldom present.

Gonophores fixed or free medusae. Medusae (when present) usually with perradial exumbrellar nematocyst tracks.

Type species: *Tubularia indivisa* Linnaeus, 1758 (Text-figs. 17, 20 & 22, pp. 468, 470 & 471).

Family MARGELOPSIDAE Uchida, 1927

Pelagic hydranths with filiform tentacles in the adult. There is an oral whorl of tentacles but the aboral one may be scattered.

Medusae with perradial groups of tentacles at bell margin or at different levels on exumbrella.

Type species: *Margelopsis haeckeli* Hartlaub, 1897 (Text-fig. 31, p. 482).

Sub-family MARGELOPSINAE Rees, 1941

Margelopsidae without a distinct float and with an aboral whorl of tentacles.

Sub-family PELAGOHYDRINAE

Margelopsidae in which the posterior half of the hydranth is modified to form a float. Aboral tentacles scattered.

Type species: *Pelagohydra mirabilis* Dendy, 1902 (Text-fig. 21, p. 470).

Super-family TRICYCLUSOIDEA nov.

Hydroids solitary with three whorls of tentacles.

This super family is created for *Tricyclusa singularis* which is a rather unique kind of hydroid which does not fit in with the *Corymorpha-Tubularia* group or with the *Acaulis-Myriothela* group, but all three groups may be said to have originated from a primitive Corymorphine stock.

Family TRICYCLUSIDAE Kramp, 1949.

Hydroids solitary with a basal anchoring disk and gelatinous sheath-like perisarc. Hydranth with an oral whorl of capitate tentacles and two aboral whorls of imperfect moniliform tentacles.

Gonophores, fixed (where known)

Type species: *Tricyclusa singularis* (Schulze, 1876) (Text-figs. 6 & 51B, pp. 462 & 505).

Super-family ACAULOIDEA nov.

Hydroids solitary, with numerous scattered capitate tentacles, and sometimes other kinds of tentacle. Perisarc either feebly developed, as a gelatinous sheath or as a chitinized tube or almost absent. Anchoring filaments are present. Gonophores, fixed (where known).

This new superfamily includes the Acaulidae and the Myriothelidae.

Family ACAULIDAE Fraser, 1924

Hydroid with gelatinous tube and anchoring filaments. Numerous capitate tentacles scattered distal to the aboral whorl of large fleshy filiform tentacles; the latter may be absent in some species.

Gonophores, fixed (where known).

Type species: *Acaulis primarius* Stimpson, 1854 (Text-fig. 13, p. 466).

Family MYRIOTHELIDAE Hincks, 1868

Hydroid with or without chitinized perisarc tube, anchored by filaments. Numerous simple or compound tentacles with or without coryniform branched tentacles which may act as blastostyles.

Gonophores fixed (where known).

Type species: *Myriothela phrygia* (Fabricius) (Text-fig. 36, p. 487).

Subfamily MONOCORYNINAE Rees, 1956[1]

Myriothelid polyp with basal perisarcal tube and a few stout anchoring filaments. Trifid capitate body tentacles. Gonophores borne in the axils of the tentacles all over the body of the polyp.

Each gonophore is hermaphroditic.

Type species: *Coryne gigantea* Bonnevie, 1898 (Text-fig. 38, p. 488).

The sole genus is *Monocoryne* Broch, 1909, with one species known only from Hammerfest and Trondheim, Norway.

Subfamily MYRIOTHELINAE nov.

Myrothelid polyp, with or without basal perisarc sheath with simple or modified anchoring filaments. Simple capitate body tentacles. Gonophores sometimes borne on special coryniform branched tentacles.

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[1] In press (*Nyt Mag. Zool. Oslo*).

Super-family Corynoidea nov.

Colonial hydroids with either a firm closely adherent perisarc, an encrusting base, or an upright rhizocaulome formation. Hydranths simple, without diaphragm and with an oral whorl of capitate tentacles.

Medusae (where present) with or without exumbrellar nematocyst tracks, with stomachs sometimes extending beyond bell margin, with simple circular mouths or with short lips armed with nematocyst clusters. Four or more radial canals with corresponding number of tentacle bulbs, with or without ocelli. Tentacles simple, bifurcating, or branched. Gonophores fixed or free medusae.

Family Asyncorynidae Kramp, 1949.

Hydranths arising from a creeping stolon. Hydranth with an oral whorl of capitate tentacles and scattered moniliform tentacles.

Gonophores fixed (where known).

Type species: *Asyncoryne ryniensis* Warren, 1908 (Text-fig. 3, p. 459).

Asyncoryne is the sole genus known and appears to have arisen independently from a primitive Corymorphine stock and has retained the moniliform tentacles.

Family Cladocorynidae Allman 1872

Hydranths borne on long perisarc-covered stems arising from creeping stolons. Oral whorl of tentacles capitate, the remainder coryniform.

Gonophores fixed (where known).

Type species: *Cladocoryne floccosa* Rotch, 1871 (Text-fig. 54, p. 511).

Family Halocordylidae Stechow, 1923

Branched upright colonies with firm tubular perisarc. Hydranths with an oral whorl of capitate tentacles, an aboral whorl of fully developed filiform tentacles, with, in addition, scattered capitate tentacles between the two whorls.

Gonophores eumedusoid (where known).

Type species: *Halocordyle tiarella* (Ayres) (Text-fig. 25 & 53, pp. 474 & 510).

Family Corynidae Johnston, 1836.

Corynoidea with upright stems, with firm perisarc, arising from creeping stolons. Hydranths, with oral capitate whorl of tentacles, usually with scattered capitate tentacles on body of hydranth, and with or without a vestigial whorl of filiform tentacles.

Fixed gonophores or free medusae. Medusae without exumbrellar nematocyst tracks, with four radial canals, four perradial tentacle bulbs with ocelli and four tentacles. Stomach with simple circular mouth.

Type species: *Coryne pusilla* Gaertner.

Family CLADONEMIDAE Allman, 1872.

Corynoidea with short stems with firm perisarc arising from creeping stolons. Hydranths with oral whorl of capitate tentacles and usually an aboral whorl of reduced filiform tentacles; without diaphragm.

Medusae with manubrium with short mouth lips armed with nematocyst clusters, with variable number of radial canals, simple or branched, and with corresponding number of tentacles. Tentacle bulbs with ocelli. Tentacles branched and with organs of adhesion.

Type species: *Cladonema radiatum* Dujardin (Pl. 12 & 13).

Family ELEUTHERIIDAE Russell, 1953.

Corynoid hydroids, with an oral whorl of capitate tentacles, with or without aboral whorl of reduced filiform tentacles.

Creeping medusae with thickened ring of nematocysts round umbrella margin. Simple circular mouth, without special armature. Radial canals variable in number, simple or branched, corresponding to number of tentacles; the latter have ocelli, organs of adhesion and may be branched. Gonads in a special brood pouch above the stomach.

Type species: *Eleutheria dichotoma* Quatrefages, 1843 (Text-fig. 48, p. 500).

Family HYDROCORYNIDAE nov.

Corynoidea with thick encrusting base. Hydranths columnar, with only an oral whorl of capitate tentacles around a conical hypostome, and with thick chitinous mesogloea.

Gonophores borne in clusters near the base of the hydranth. Newly liberated medusa (where known) with deep bell shape, four radial canals and four tentacles each with swollen bulb and ocellus. Stomach short with simple circular mouth.

Type species: *Hydrocoryne miurensis* Stechow, 1907 (Text-fig. 49, page 500).

Family PTILOCODIIDAE Coward, 1909.

Corynoidea with naked anastomosing stolons forming a continuous coenosarc. Nutritive polyps without tentacles, dactylozooids with one whorl of capitate tentacles.

Gonophores fixed (where known) borne at the base of the nutritive zooid.

Type species: *Ptilocodium repens* Coward, 1909 (Text-fig. 55, page 513).

Family SOLANDERIIDAE Marshall, 1892.

Corynoid colonies with mesogloeal skeleton, either in the form of an encrusting base, or as anastomosing branches, completely enclosed in ectoderm. Hydranths with scattered capitate tentacles.

Gonophores fixed (where known) arising directly from the coenosarc and not from the body of the hydranth.

Type species : *Solanderia gracilis* Duchassaing & Michelin.

Family ZANCLEIDAE Russell, 1953.

Hydroids with irregularly distributed tentacles, either all capitate, or all filiform, or of both types.

Anthomedusae with, or without, exumbrella nematocysts confined to specialized tissue in the form of oval or club-shaped patches or elongated tracks, with simple circular mouth ; with four radial canals ; with inter-radial gonads ; with two or four hollow marginal tentacles, each with abaxial stalked capsules (or cnidophores) containing nematocysts, or without marginal tentacles ; without ocelli.

Type species : *Zanclea costata* Gegenbaur (Text-fig. 47, p. 499).

The above definition was given by Russell (1953). In *Pteroclava* the filiform tentacles are actually slightly club-shaped and it appears likely that they are capitate when young. Consequently they have not been mentioned in the definition of the super-family (see p. 516 for a discussion of the family's status).

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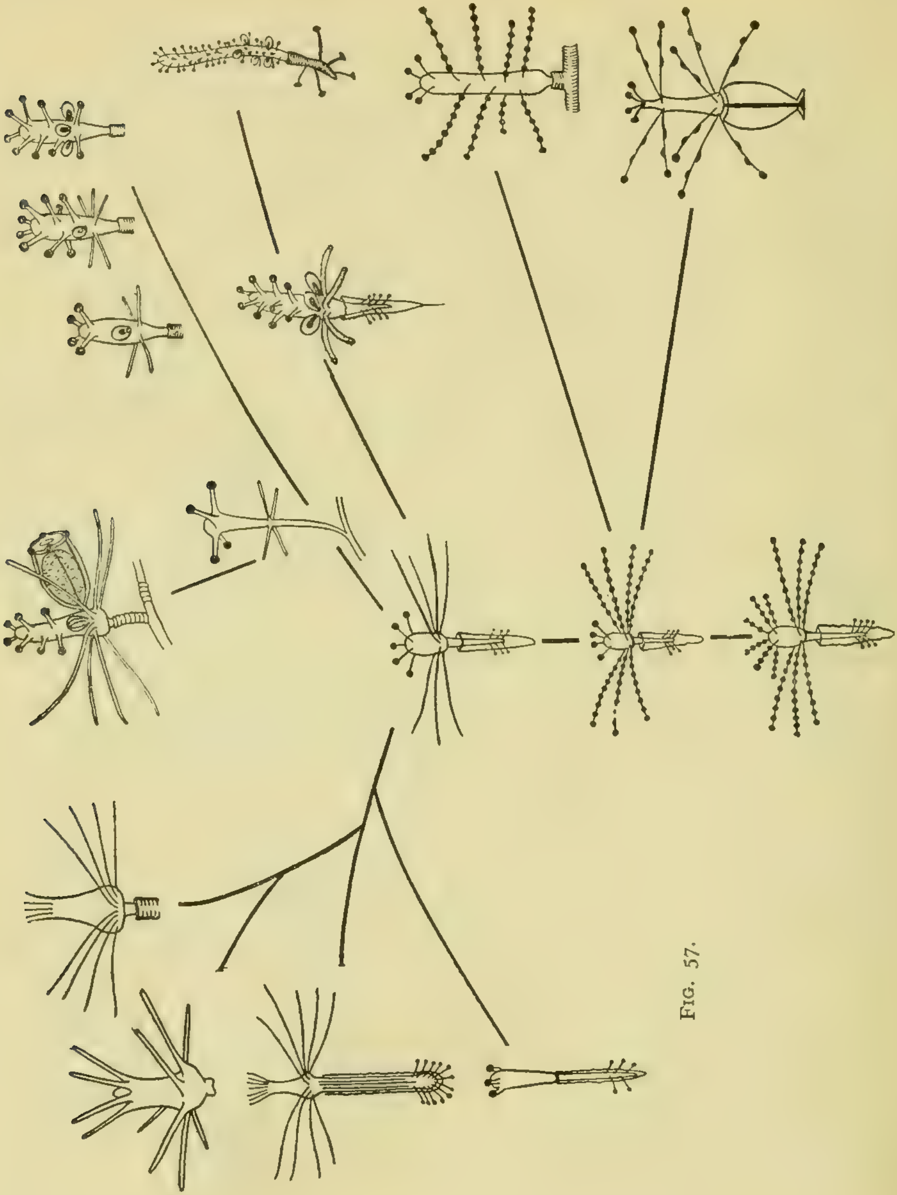

FIG. 57.

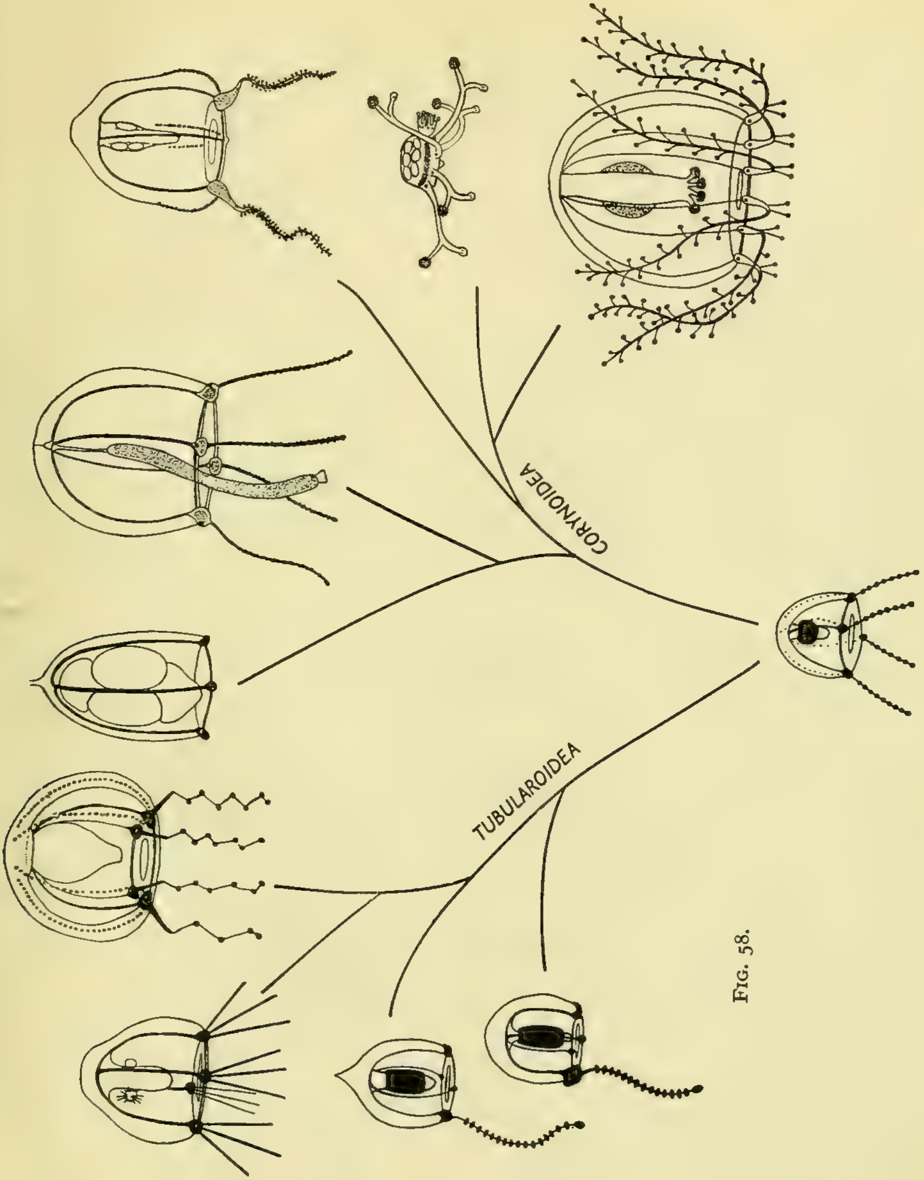
CORYNOIDEA
TUBULAROIDEA

FIG. 58.

EXPLANATION OF FIGURES AND PLATES

Fig. 57. A diagrammatic representation of the main evolutionary trends in capitate hydroids in which the different hydroid types are represented by stylized sketches representing groups rather than individual species.

Fig. 58. Relationships of the different codonoid medusae; it will be noted that some aberrant Corynoid medusae have been included and that no medusae are known in the Tricyclusoidea and the Acauloidea.

PLATES 12 AND 13

Cladonema radiatum Dujardin

Photographs of living polyps and medusae taken by the shadowgraph method by the late Mr. O. E. Challis from colonies maintained in aquaria by Mr. F. J. Lambert, Leigh-on-Sea, Essex.

PLATE 12

Fig. 1. Typical sterile polyp with four oral capitate tentacles and four filiform aboral tentacles.

Fig. 2. Another polyp with six oral tentacles and a young medusa bud.

Fig. 3. The same hydranth as in Figure 2 with the medusa nearly ready for liberation.

Fig. 4. Another hydranth reduced to a blastostyle with one fully developed medusa.

PLATE 13

Cladonema radiatum Dujardin

Fig. 5 and 6. Different views of the medusa, seen in Plate 1, fig. 4, prior to liberation. Note that the blastostyle is completely reduced.

Fig. 7 and 8. Two views of the sexually mature medusa.

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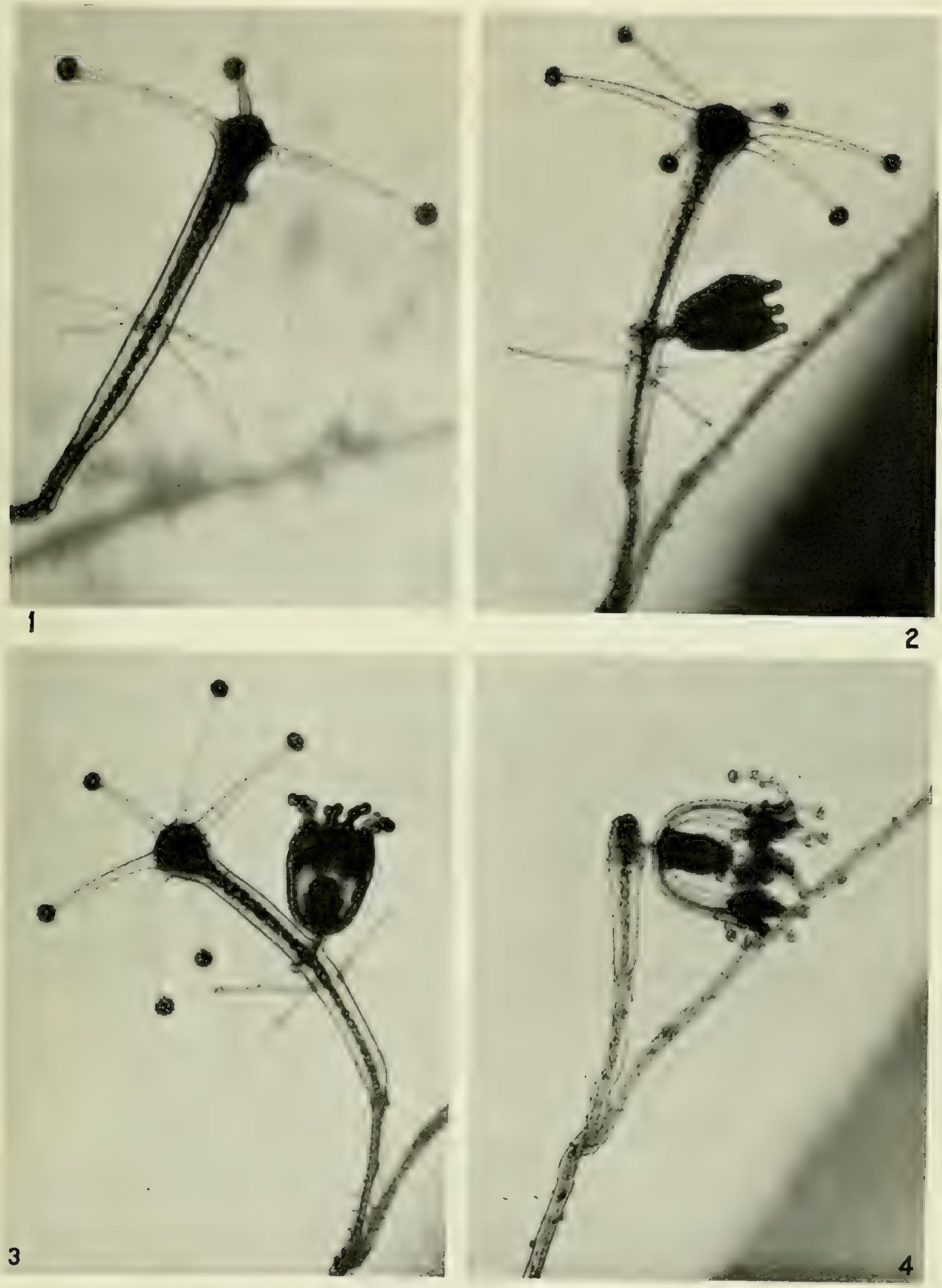

Cladonema radiatum Dujardin.

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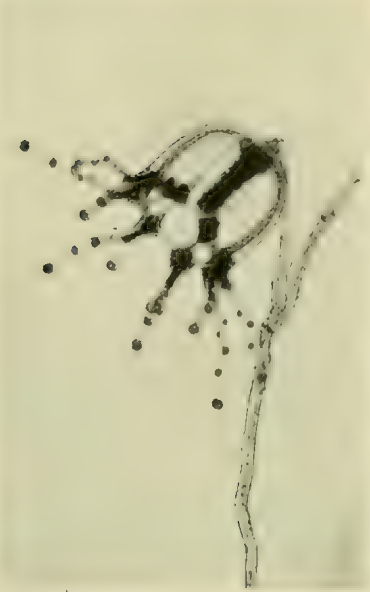

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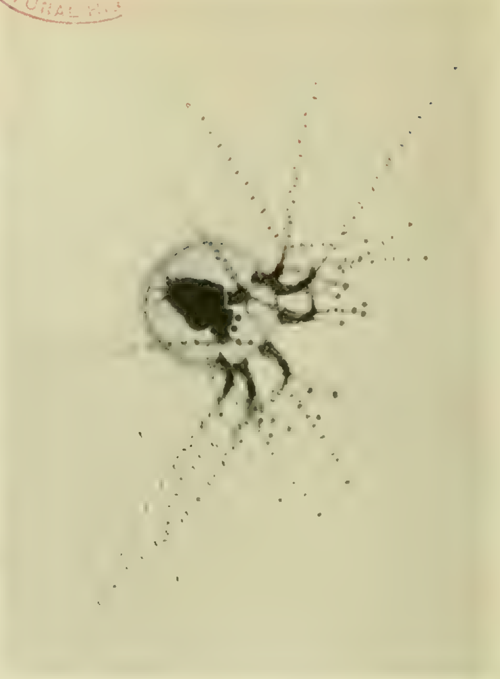

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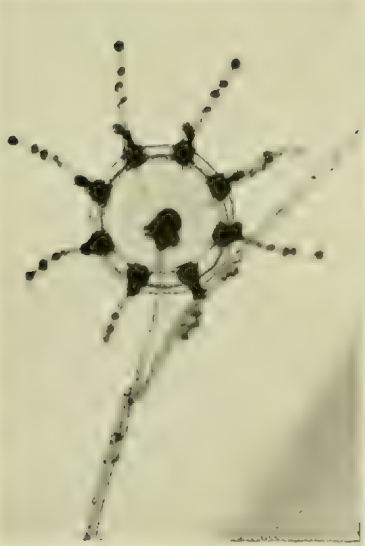

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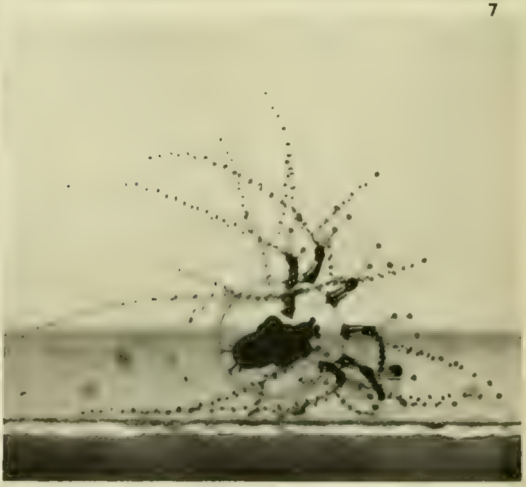

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Cladonema radiatum Dujardin.

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